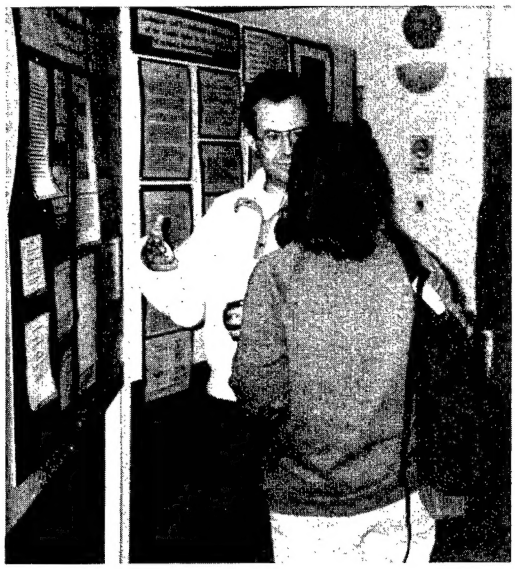
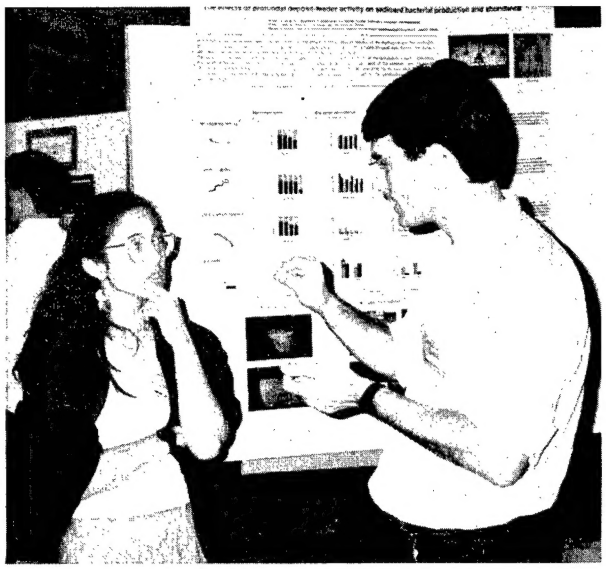
# American Society of Limnology and Oceanography

# Dissertations Initiative for the Advancement of Limnology and Oceanography (DIALOG)

## June 1, 1992 - September 1, 1994
## Ph.D. dissertation abstracts





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ROBERT J. SILVERMAN

December 18, 1995

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Sincerely,

C. Susan Weiler

C. Susan Weiler, Ph.D.
Principal Investigator

## American Society of Limnology and Oceanography

# Dissertations Initiative for the Advancement of Limnology and Oceanography (DIALOG)

## Ph.D. Dissertation Abstracts of Applicants Completing Their Ph.D. Degree between June 1, 1992 and September 1, 1994


***Supported by:***

**National Science Foundation**
*Biological Oceanography Program*
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*Biological and Chemical Oceanography Program*

## ACKNOWLEDGMENTS

The Dissertations Initiative for the Advancement of Limnology and Oceanography (DIALOG) program was developed through the American Society of Limnology and Oceanography (ASLO) to foster inter-disciplinary and inter-institutional research and interactions among aquatic scientists. The Dissertations Symposium in Chemical Oceanography (DISCO) program, originally conceived by **Edward D. Goldberg**, was used as a model. ASLO is particularly grateful to the DISCO program organizer, **Mary-Frances Thompson** (American Inst. Biological Science), for sharing her experience, and to **Edward Green** (Office of Naval Research) for inviting me, as the DIALOG program organizer, to observe the DISCO XII symposium.

On behalf of ASLO and the larger aquatic science community, I thank members of the DIALOG Steering Committee (**Jonathan J. Cole** (Institute of Ecosystem Studies), **Carol L. Folt** (Dartmouth College), **Eileen E. Hofmann** (Old Dominion University), **Peter A. Jumars** (University of Washington), **Chris M. Luecke** (Utah State University), **Anthony F. Michaels** (Bermuda Biological Station for Research), **Jonathan H. Sharp** (University of Delaware), **Michael J. Vanni** (Miami University), **Bess B. Ward** (University of California at Santa Barbara), **C. Susan Weiler** (Chair, Whitman College), and **Craig E. Williamson** (Lehigh University)) for developing this program targeting recent Ph.D. recipients in limnology and oceanography.

The DIALOG '94 Symposium Committee (**Jonathan J. Cole, Larry B. Crowder** (North Carolina State University), **Paul J. Harrison** (University of British Columbia), **Anthony F. Michaels, Bess B. Ward, C. Susan Weiler** (Chair), and **Craig E. Williamson**) selected participants for the symposium, finalized the symposium format, and recommended symposium mentors from a list of mid-career scientists nominated by the DIALOG '94 applicants. We congratulate and thank **Cindy Lee** (State University of New York at Stony Brook) for being selected and serving as Mentor for this first program. Her insights and perspectives throughout the symposium were much appreciated. We thank **Russell A. Moll** (NSF) for representing NSF and for collaborating with Cindy Lee on a session dealing with research careers, and **Leon M. Cammen** (NOAA), **Robert J. Frouin** (NASA) and **Eric Shulenberger** (ONR) for representing their agencies and programs at the symposium. We also thank **Mary A. Meeker** (Whitman College) for logistical support and data base management, and **Margaret Potts** and the rest of the staff at the Bermuda Biological Station for Research for their friendly and efficient handling of on-site logistics, meals and housing for the symposium participants.

Support for the DIALOG program was provided by the **National Science Foundation** (Biological Oceanography, Ecosystems Studies, and Polar Biology & Medicine Programs), **National Oceanic and Atmospheric Administration** (Coastal Oceanography Program and Office of Oceanic & Atmospheric Research), **National Aeronautics and Space Administration** (Ocean Biogeochemistry Program and Atmospheric Chemistry & Ecology Branch, Mission to Planet Earth Program) through NSF grant OCE-9319740 to Whitman College, and the **Office of Naval Research** (Biological and Chemical Oceanography Program), through ONR R&T Project Code 22BA 249---01 to Whitman College. We thank **Phillip R. Taylor, Richard F. Dame, Penelope Firth, Roger B. Hanson**, and other members of NSF's Limnos group for their early encouragement, and **Phillip R. Taylor** (NSF) and **William F. Graham** (NOAA) for facilitating the interagency cooperation. Support does not constitute an endorsement of the contents by any supporting agency.

C. Susan Weiler, Executive Director
American Society of Limnology and Oceanography
January 15, 1995

# CONTENTS

# INTRODUCTION

The DIALOG Program was founded by the American Society of Limnology and Oceanography (ASLO), in order to reduce the historical, institutional and philosophical barriers that limit the exchange of information between limnologists and oceanographers, and to foster interdisciplinary and inter-institutional research. This was achieved by targeting a recent cohort of Ph.D. recipients whose work included a biological component of limnology or oceanography. The program included:

- Publication of the submitted Ph.D. dissertation abstracts;
- a symposium to facilitate exchange across institutions and disciplines; and
- establishment of a centralized data base for applicant characterization and tracking.

Program announcements were sent out to the ca. 3,800 members of the American Society of Limnology and Oceanography (ASLO) and to the heads of departments of the ca. 1,300 academic institutions throughout the world which subscribe to *Limnology and Oceanography*. In addition, announcements were sent to a variety of professional scientific societies, including the American Geophysical Union, British Ecological Society, Ecological Society of America, Estuarine Research Federation, International Association for Great Lakes Research, International Association for Theoretical and Applied Limnology, North American Benthological Society, North American Lake Management Society, and the Society of Canadian Limnologists. The program was open to those completing their final dissertation requirement between June 1, 1992 and September 1, 1994.

A total of 80 applications were received. Applicants were categorized as limnologists or oceanographers according to the *primary area of their dissertation research* (several have worked in both marine and freshwater environments, and many have joint interests). Fifty three of the applicants (42 U.S. citizens and 11 non-U.S. citizens) received their highest degree from U.S. institutions (Table I). These 80 **Program Applicants** included:

28 (35%) limnologists
52 (65%) oceanographers
28 (35%) females
52 (65%) males
42 (53%) U.S. citizens: 27 (64%) male, 15 (36%) female;
10 (24%) limnologists, 32 (76%) oceanographers.
10 (12%) Canadians
28 (35%) citizens of other countries (Brazil 1; Chile 3; China 1; Denmark 1; Germany 3; Ireland 1; Israel 1; Italy 2; Kenya 1; Mexico 2; Netherlands 4; Spain 5; Switzerland 1; Turkey 1; and United Kingdom 1).

Oceanographers represented the majority of applicants among U.S. citizens (32 oceanographers and 10 limnologists) and among applicants with degrees from U.S. institutions (53 total; 14 limnology and 39 oceanography), while the proportion of limnologists and oceanographers was more evenly split among non-U.S. applicants with degrees from institutions outside the U.S. and Canada (Table II; 15 oceanographers and 13 limnologists). The low proportion of U.S. limnologists was unexpected. With more than 3,800 members worldwide, ASLO membership includes roughly equal numbers of limnologists and oceanographers. Based on this, the organizers anticipated that comparable proportions of limnologists and oceanographers would apply to the program.

Table II compares the number and proportion of limnologists among the ASLO U.S. student membership (43%) and among the U.S. DIALOG applicants (24%). It is not known whether difference reflect the proportion of limnologists and oceanographers graduating, differences in interest or awareness of the DIALOG program among groups or an artifact of small sample size.

The age distribution of applicants at time of Ph.D. is presented in Fig. 1. The mean, median, and range of ages of applicants during the year his/her Ph.D. degree was completed (year Ph.D. awarded - year of birth) were: 33, 32 and 25 - 43 years for U.S. applicants: and 34, 32 and 28 - 48 years for applicants from outside the United States.

Sixty-eight applicants requested to be considered for the symposium, while 12 did not. The 68 **symposium applicants** included:
23 (34%) limnologists
45 (66%) oceanographers
23 (34%) females
45 (66%) males
39 (57%) U.S. citizens
10 (15%) Canadian citizens
19 (28%) citizens of other countries (Brazil 1; Chile 3; China 1; Germany 2; Ireland 1; Israel 1; Italy 2; Netherlands 3; Mexico 1; Spain 2; Turkey 1; and United Kingdom 1).

Symposium participation was limited to 41 individuals. The selection committee considered the following materials: 1-page thesis abstract; 1-page description of career goals, interdisciplinary interests, and ways in which participation would enhance professional growth and contribute to the symposium; 2-page CV; and two letters of recommendation. Each committee member read and evaluated each of the 68 applications. These were discussed and final decisions were made during a 1-day meeting in Washington, DC. Selection was difficult due to the high quality of all applicants. Program balance and other criteria were considered, and preference was given to those with a demonstrated interest in interdisciplinary research and publication. The 41 **symposium participants** included:
15 (37%) limnologists
26 (63%) oceanographers
16 (39%) females
25 (61%) males
26 (63%) U.S. Citizens
7 (17%) Canadian citizens
8 (20%) citizens of other countries

All submitted dissertation abstracts are presented here to provide a concise introduction to the work of this most recent generation of aquatic science researchers, and to facilitate communication within and across disciplines. The compilation includes:
- Index with dissertation citations arranged alphabetically by last name
- Dissertation abstracts, arranged alphabetically by last name
- Directory of applicants, including
  -- name, address, phone and fax number, and e-mail address
  -- primary field of dissertation research (limnology *or* oceanography)
  -- up to three key words, describing areas of research interest and expertise.

**Table I.** Institutions granting Ph.D. degrees to 1994 DIALOG program applicants. Dissertation fields are listed as lim or oce, based on the primary area of dissertation research.

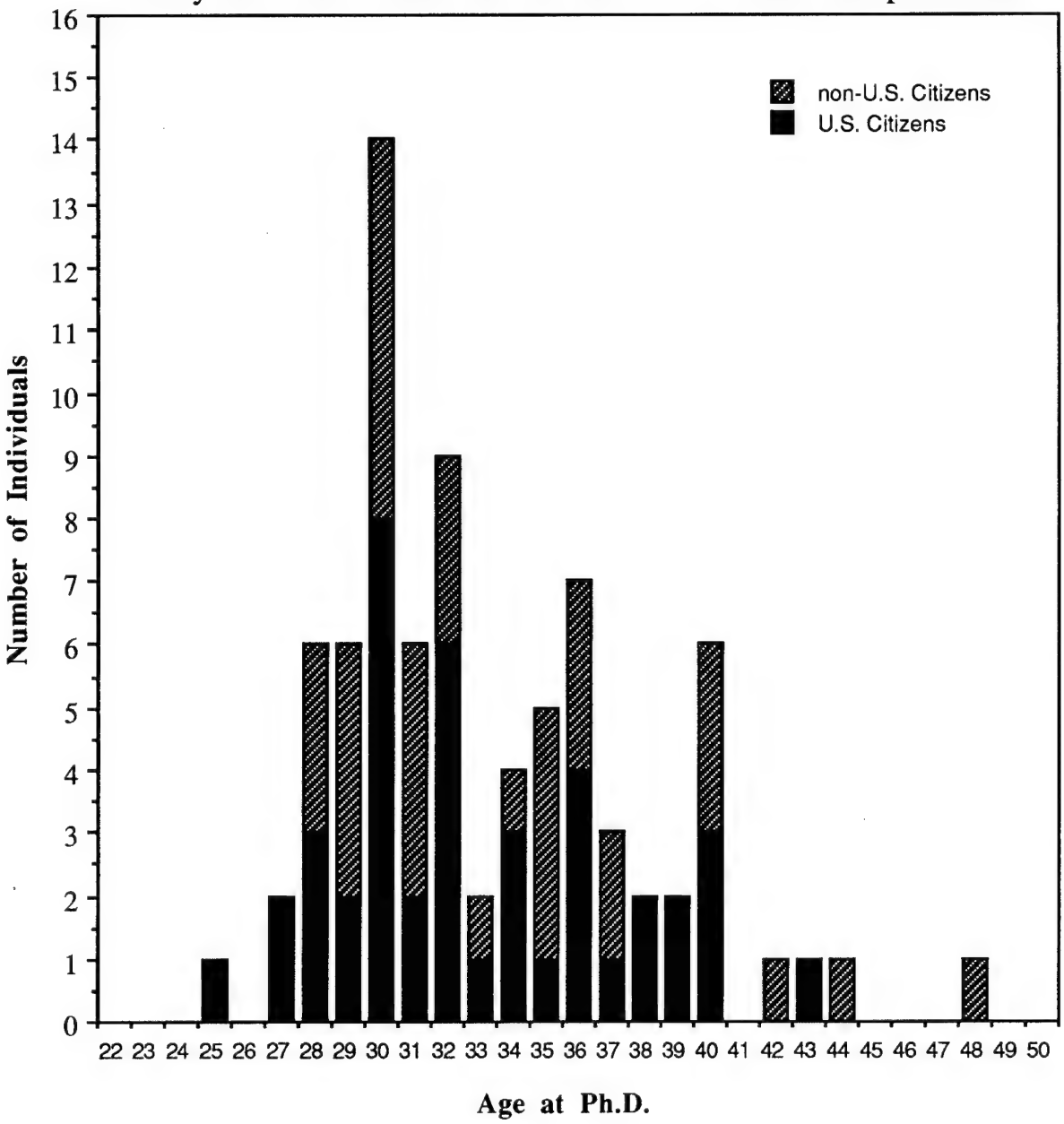
| Lim | Oce | U.S. Institutions: |
|---|---|---|
| 2 | 0 | Dartmouth College |
| 0 | 1 | Duke Univ. |
| 0 | 1 | Florida Institute Technology |
| 1 | 1 | George Mason Univ. |
| 1 | 0 | Iowa State Univ. |
| 0 | 1 | Johns Hopkins Univ. |
| 0 | 2 | Louisiana State Univ. |
| 0 | 1 | Massachusette Inst Technology |
| 1 | 0 | Michigan Technological Univ. |
| 1 | 0 | Michigan State Univ. |
| 0 | 1 | Mississippi State Univ. |
| 0 | 2 | Oregon State Univ. |
| 0 | 1 | Stanford Univ. |
| 1 | 1 | State Univ. New York , Stony Brook |
| 0 | 1 | Texas A&N Univ. |
| 1 | 0 | Univ. California at Davis |
| 0 | 6 | Univ. California at San Diego |
| 1 | 1 | Univ. California at Santa Barbara |
| 0 | 5 | Univ. California at Santa Cruz |
| 0 | 1 | Univ. Delaware |
| 1 | 0 | Univ. Florida |
| 0 | 2 | Univ. Hawaii at Manoa |
| 0 | 1 | Univ. Maine |
| 0 | 2 | Univ. Maryland at College Park |
| 0 | 3 | Univ. North Carolina at Chapel Hill |
| 0 | 1 | Univ. Rhode Island |
| 0 | 2 | Univ. South Carolina |
| 0 | 2 | Univ. Washington |
| 1 | 0 | Univ. Wisconsin at Madison |
| 2 | 0 | Univ. Wisconsin at Milwaukee |
| 1 | 0 | Yale Univ. |
| **14** | **39** | **TOTAL** |

| Lim | Oce | Non-U.S. Institutions: |
|---|---|---|
| 0 | 1 | Bar-Ilan Univ. (Israel) |
| 0 | 3 | Dalhousie Univ. (Canada) |
| 1 | 0 | Queen's Univ. (Canada) |
| 0 | 1 | Middle East Tech. Univ. (Turkey) |
| 1 | 0 | Politecnico di Milano (Italy) |
| 1 | 0 | Rostock Univ. (Germany) |
| 3 | 0 | Univ. Amsterdam (Netherlands) |
| 0 | 1 | Univ. Copenhagen (Denmark) |
| 1 | 0 | Univ. Hamburg (Germany) |
| 1 | 1 | Univ. Kiel (Germany) |
| 1 | 1 | Univ. Laval (Canada) |
| 1 | 0 | Univ. Manatoba (Canada) |
| 0 | 1 | Univ. Nairobi (Kenya) |
| 0 | 1 | Univ. Plymouth (United Kingdom) |
| 0 | 1 | Univ. South Hampton (United King.) |
| 3 | 0 | Univ. Valencia (Spain) |
| 0 | 1 | Univ. Victoria (Canada) |
| 0 | 1 | Univ. Western Ontario (Canada) |
| 1 | 0 | Vrije Univ. (Netherlands) |
| **14** | **13** | **TOTAL** |

**Table II.** The number and percentage of limnologists and oceanographers (as indicated by the primary area of Ph.D. dissertation research) is shown for 1994 and 1995 ASLO student members and for the 1994 DIALOG program applicants.

| Lim | Oce | Total | Group |
|---|---|---|---|
| | | | **ASLO** |
| 322 (43%) | 434 (57%) | 756 | student members, United States |
| 67 (64%) | 37 (36%) | 104 | student members, Canada |
| 81 (49%) | 83 (51%) | 164 | student members, all other Countries |
| | | | **DIALOG Applicants** |
| 10 (24%) | 32 (76%) | 42 | U.S. citizens |
| 3 (30%) | 7 (70%) | 10 | Canadian citizens |
| 15 (53%) | 13 (46%) | 28 | other citizenship |
| 14 (26%) | 39 (74%) | 53 | Ph.D. degrees from U.S. institutions |
| 3 (33%) | 6 (67%) | 9 | Ph.D. degrees from Canadian institutions |
| 11 (61%) | 7 (39%) | 18 | Ph.D. degrees from other institutions |

Fig. 1. Age at Ph.D. for DIALOG applicants (year Ph.D. awarded - year of birth). Forty-two U.S. citizens and 38 non-U.S. citizens are represented.



# Ph.D. Dissertation Index

17 **Dekker, Arnold G. 1993.** Detection of optical water quality parameters for eutrophic waters by high resolution remote sensing. Vrije University (Netherlands), 222 pp.

18 **Deslarzes, Kenneth J.P.** 1992. Long-term monitoring of reef corals at the Flower Garden Banks (northwest Gulf of Mexico): Reef coral population changes and historical incorporation of barium in *Montastrea annularis*. Texas A&M University, 170 pp.

19 **Dickson, Mary-Lynn.** 1994. Nitrogen dynamics in a coastal upwelling regime. Oregon State University, 227 pp.

20 **Douglas, Marianne S.V.** 1993. Diatom ecology and palelimnology of high Arctic ponds. Queen's University (Canada), 161 pp.

21 **Dower, John F.** 1994. Biological consequences of current-topography interactions at Cobb Seamount. University of Victoria (Canada), 231 pp.

22 **Edmands, Suzanne.** 1994. Genetic and evolutionary consequences of various reproductive strategies in the sea anemone Genus *Epiactis*. University of California at Santa Cruz, 187 pp.

23 **Esparcia, C. Angeles.** 1993. Rotifer population distribution in the oxycline of "la laguna de las Cruz": Metabolic adaptations of *Bachionus plicatilis* to microaerobic conditions. University of Valencia (Spain), 288 pp.

24 **Ferrier, M. Drew.** 1992. Fluxes and metabolic pools of amino acids in algal-cnidarian symbioses. University of Maryland at College Park, 177 pp.

25 **Frenette, Jean-Jacques.** 1993. Impact of hydrodynamic factors on photosynthesis and the fate of primary production in an oligotrophic lake. University of Laval (Canada), 177 pp.

26 **Giovannini, Phillip.** 1994. Water quality dynamics in aquaculture ponds: An investigation of photosynthetic production and efficiency variations. University of California at Davis, 192 pp.

27 **Graham, William M.** 1994. The physical oceanography and ecology of upwelling shadows. University of California at Santa Cruz, 205 pp.

28 **Haberstroh, Paul R.** 1994. Wave-forced porewater mixing and nutrient flux in a coral reef framework. University of Hawaii at Manoa, 249 pp.

29 **Hamblin-Katnik, Claudia.** 1993. USEPA water quality criteria for copper: I. Exceedence of criteria in freshwater streams. II. Influence of dissolved organic matter on toxicity. George Mason University, 203 pp.

30 **Hare, Jonathan A.** 1994. Biological and physical processes affecting the larval survival and esturarine recruitment of bluefish, *Pomatomus saltatrix*, (Pisces: Pomatomidae), along the eastern coast of the United States. State University of New York at Stony Brook, 264 pp.

31 **Hu, Shixi S.** 1994. Competition in a seasonal environment: *Daphnia* population dynamics and coexistence. Michigan State University, 109 pp.

32 **Hutchins, David A.** 1994. Regeneration and recycling of biologically required trace metals by marine plankton communities. University of California at Santa Cruz, 91 pp.

33 **Ibelings, Bastiaan W.** 1992. Cyanobacterial waterblooms: The role of buoyancy in water columns of varying stability. University of Amsterdam (Netherlands), 171 pp.

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35 **Jack, Jeffrey D.** 1993. Direct and indirect effects on planktonic ciliate assemblages. Dartmouth College, 185 pp.

36 **Joye, Samantha B.** 1993. Spatial and temporal patterns of nitrogen fixation and denitrification in the intertidal and subtidal sediments of a Mediterranean-type estuary: Tomales Bay, California. University of North Carolina at Chapel Hill, 227 pp.

37 **Jungmann, Dirk.** 1994. Toxic secondary metabolites from *Microcystis* flos-aque strain PCC7806: Biochemical characterization by natural and laboratory investigations. University of Kiel (Germany), 101 pp.

38 **Kostka, Joel E.** 1992. Biogeochemical cycling of iron in anoxic environments: The importance of Fe speciation and bacterial Fe reduction. University of Delaware, 243 pp.

39 **Lindley, Steven T.** 1994. Regulation of the maximum quantum yield of phytoplankton photosynthesis by iron, nitrogen, and light in the eastern equatorial Pacific. Duke University, 136 pp.

40 **Mayer, Marilyn S.** 1992. Effects of benthic macrofauna on nitrogen cycling and oxygen consumption of estuarine sediments. University of Maryland at College Park, 182 pp.

41 **Mehner, Thomas.** 1992. Ecological investigations of the age-0 fish community in a shallow brackish water of the southern Baltic. Rostock University (Germany), 139 pp.

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43 **Miller, Margaret W.** 1994. Ecology of a temperate coral. University of North Carolina at Chapel Hill, 157 pp.

44 **Miller-Way, Christine A.** 1994. The role of infaunal and epifaunal suspension feeding macrofauna on rates of benthic-pelagic coupling in a southeastern estuary. Louisiana State University, 203 pp.

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47 **Muelbert, Jose H.** 1994. The relevance of feeding environment to "retention" of Atlantic herring (*Clupea harengus*) larvae. Dalhousie University, (Canada), 152 pp.

48 **Murray, Alexander, G.** 1993. Modelling investigations of marine microplankton ecology. University of Southhampton (United Kingdom), 387 pp.

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50 **Oltra, Rafael.** 1993. Study of zooplankton in two Mediterranean coastal lagoons: The Estany of Cullera and the Albufera of Valencia (Spain). University of Valencia (Spain), ?pp.

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53 **Oyieke, Helida A.** 1993. A taxonomic, ecological and commercial potential study of the genus *Gracilaria* (Gracilariaceae, Rhodophyta) of the Kenya coast. University of Nairobi (Kenya), 281 pp.

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55 **Palowitch, Andrew W.** 1994. Chlorophyll: A spatial microstructure determination from volumetrically reconstructed optical serial sectioned fluorescence images. University of California at San Diego, 139 pp.

56 **Pan, Youlian.** 1994. Production of domoic acid, a neurotoxin, by the diatom *Pseudonitzschia pungens* f. multiseries (Hasle) under phosphate and silicate limitation. Dalhousie University (Canada), 245 pp.

57 **Pape-Lindstrom, Pamela A.** 1994. A laboratory and field study of sublethal predation on the brittlestar, Microphiopholis gracillima, (Stimpson) (Echinodermata: Ophiuroidae), by white shrimp and other macerating preditors: An immunochemical approach. University of South Carolina, 136 pp.

58 **Perez-Fuentetaja, Alicia.** 1993. Effects of fish on planktonic communities and food web response to varying predation pressures and nutrient regimes. State University of New York at Syracuse, 135 pp.

59 **Pinckney, James L.** 1992. Ecology of intertidal benthic microalgal communities in North Inlet Estuary, South Carolina. University of South Carolina, 276 pp.

60 **Pineda, Jesús.** 1993. Hydrodynamic forcing on shallow water communities: Some physical effects and ecological consequences of internal tidal bores. University of California at San Diego, 158 pp.

61 **Pinto, Luis, A.** 1993. The role of sulfur in the preservation of isoprenoid hydrocarbons in sedimentary materials of the Washington Continental Margin. Oregon State University, 220 pp.

62 **Pollice, Alfieri.**1994. Experimental validation of a model for biological nutrient removal in activated sludge plants. Politecnico di Milano (Italy), 284 pp.

63 **Powell, David E.** 1993. Cadmium accumulation in the bottom sediments and fish of seepage lakes in north-central Wisconsin: Relation to lake chemistry. Iowa State University, 126 pp.

64 **Richter, Claudio.** 1994. Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. University of Kiel (Germany), 101 pp.

65 **Rood, Brian E.** 1993. Spatial and temporal distribution of mercury and other trace metals in Florida Everglades and Savannas Marsh flooded soils. University of Florida, 180 pp.

66 **Ruiz, Jose M.** 1993. Metallic pollution in estuaries, with special reference to the effects of tributyltin (TBT) and copper on the early life stages of *Scrobicularie plana* (Mollusca: Bivalvia). University of Plymouth (United Kingdom), 167 pp.

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72 **Stambler, Noga.** 1992. Harvesting and utilization of light by Hermatypic corals. Bar-Ilan University (Isreal), 221 pp.

73 **Steinberg, Deborah K.** 1993. The use of mesopelagic detritus by zooplankton in Monterey Bay, California. University of California at Santa Cruz, 163 pp.

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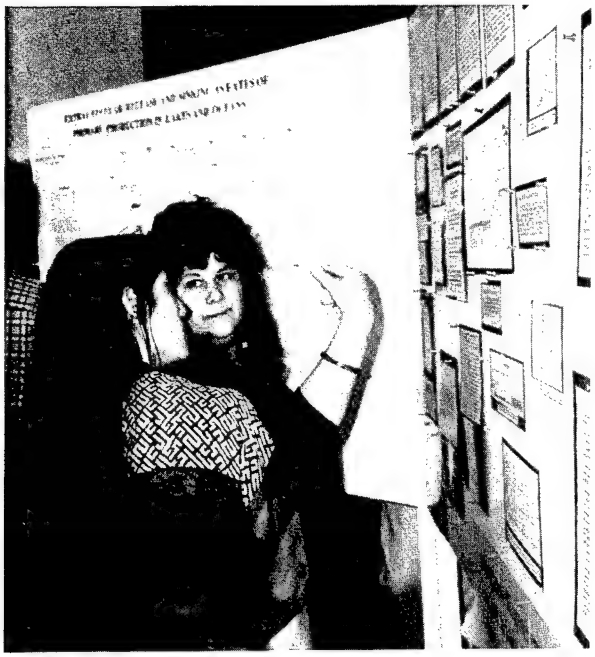
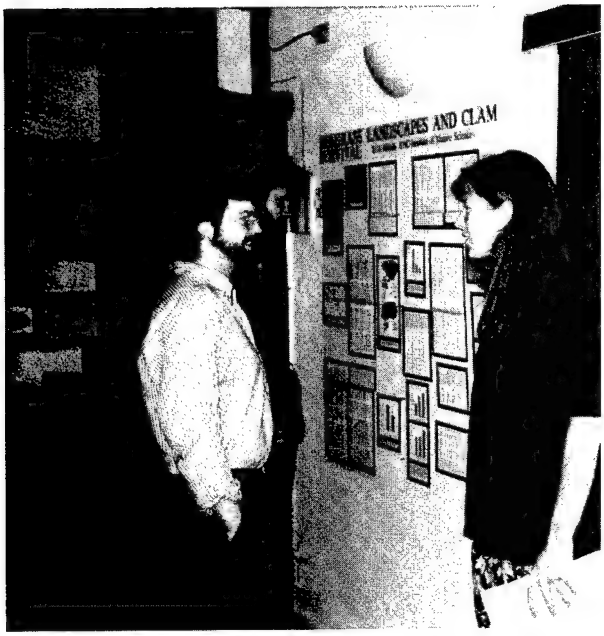
77 **van de Bund, Wouter J.** 1994. Food web relations of littoral macro- and meiobenthos. University of Amsterdam (Netherlands), 107 pp.

78 **Verde, E. Alan. 1993.** The effects of temperature, light, season, and body size on the photosynthesis and respiration of zooxanthellae and zoochlorellae symbiotic within *Anthopleura elegantissima* (Brandt). Florida Institute of Technology, 86 pp.

79 **Wilhelm, Steven W.** 1994. Ecological aspects of iron acquisition in *Synechococcus* spp. (Cyanophyceae). University of Western Ontario (Canada), 196 pp.

80 **Wiltshire, Karen H.** 1991. Investigations into the influence of microphytobenthos on nutrient exchange between sediments and water in the tidal Elbe. University of Hamburg (Germany), 186 pp.




LANDSCAPES AND CLAM

# Satellite Imagery of Danish and Neighboring Waters: Interpretation of Satellite Ocean Color Data of the Transition Zone Between the North Sea and the Baltic Sea

**Aarup, T. 1994**
**University of Copenhagen (Denmark), 162 pp.**

The transition area between the North Sea and the Baltic Sea has attracted much interest in recent years due a number of environmental "events". In the Kattegat, large oxygen-depleted areas have been found in the late summer months during the 1980's. Oxygen-depleted areas have also been observed along the Danish west coast and in the German Bight . In the Skagerrak and the Kattegat, toxic algae blooms have been seen with irregular occurrences over the years (one of the most "famous" was the *Chrysochromulina polylepis* bloom that took place in May and June of 1988).

The Skagerrak is one of the least-studied sea areas in the North Sea - Baltic Sea region and there is a great deal of controversy regarding the exchange of water with the North Sea/Kattegat/Baltic Sea, the internal circulation, and the general ways of transport of substances. Little use has been made of the arhive of CZCS images for this region. The aim of this study was: 1) to process available CZCS imagery and matching AVHRR scenes of the transition zone between the North Sea and the Baltic Sea; 2) to interpret the imagery in relation to matching in situ data; and 3) to analyze (mainly from a remote sensing point of view) bio-optical measurements gathered during nine cruises from 1990-92 in the eastern North Sea, the Skagerrak and the Kattegat.

The imagery shows that: 1) coccolithophores are transported into the Skagerrak from the central and northern North Sea during the summer, and cover large areas of the Skagerrak; 2) water from the Norwegian Coastal Current can at times be spread further south than previously anticipated; 3) during the months of February-October the Skagerrak-Kattegat front is typically aligned in the direction of Skagen-Marstrand or slightly north of there; and 4) the surface layer of the Kattegat is optically fairly homogeneous on a horizontal scale.

The light data has been used to describe the underwater light climate and its spatial and seasonal variations in the study region and to develop satellite ocean color algorithms for estimation of water quality parameters. Empirical relations were established between the vertical attenuation coefficients Kd(.) and Kd(488) which showed good agreement with the results obtained by Austin & Petzold (1986).

It is argued that the irradiance attenuation coefficient Kd(410) can be taken as a good indicator of yellow stuff in the study region. Salinity - Kd(410) scatter plots show that three water types can be identified in the area: Atlantic/Central North Sea water; German Bight water; and Baltic water. This is in contrast to classical temperature-salinity analysis that only allows two water masses to be identified. Estimates of the mean width of the part of the Jutland Coastal Current (Eastern North Sea) that primarily is influenced by the freshwater inflow to the German Bight are given for fixed sections along the Danish west coast. Salinity - yellow stuff water mass analysis was carried out on the measurements from this study based on long term mean characteristic values of salinity and yellow stuff for the above three core water types.

The average contents of Atlantic/Central North Sea water, German Bight water and Baltic water was estimated for the surface layer at three fixed sections along the Danish west coast. Based on the volume flow estimates from the three sections, an estimate of the mean volume flow of water with German Bight origin entering the Skagerrak is given.

# Biogeochemical Cycling of Manganese in Oneida Lake, New York

**Aguilar, C.D. 1992**
**University of Wisconsin at Milwaukee, 360 pp.**

The biogeochemical manganese cycling in Oneida Lake, N.Y. is the focus of this dissertation. The involvement of manganese in biological, physical and chemical interactions determines the spatial and temporal distribution of this biologically active trace metal. In the aquatic environment, the most commonly found oxidation states of manganese were Mn(II), Mn(III) and Mn(IV). Evidence is presented implicating microbial rather than purely chemical mechanisms in oxidation-reduction conversions among manganese species.

The results from studies of the different aspects on manganese biogeochemistry provided persuasive evidence for the following scenario for the manganese cycle in Oneida Lake:

a) Soluble manganese Mn(II), was oxidized by certain cyanobacteria, particularly Microcystis aeruginosa and Anabaena circinalis. The quantitative oxidation of micromolar concentrations of reduced manganese was driven by the photosynthetically induced increases in local dissolved oxygen concentration and pH in the vicinity of cells and cyanobacterial aggregates.

b) Sedimentation of the manganese oxide-coated cyanobacteria rapidly transported particulate manganese to the sediment surface. Depositional zone sediments are anoxic within a few mm of the surface.

c) Manganese reducing bacteria metabolize the manganese oxides releasing soluble, reduced manganese. Microbially-mediated reduction by organisms such as Shewanella putrefaciens probably accounts for a large proportion of the manganese reduction that occurs in the sediments, chemical reduction is important late in the summer. The concomitant oxidation of organic matter couples the manganese and carbon cycles remineralizing the phytoplanktonic biomass.

d) During episodes of calm weather, transient stratification and subsequent development of anoxic conditions promoted diffusion of soluble manganese into the hypolimnion, with concentrations exceeding 20 μM in many instances.

e) Reoxidation of manganese by manganese oxidizing bacteria was widely present in oxic, non-depositional zones in shoals areas, adjacent to the reducing depositional zones of the hypolimnion.

f) Accretion of particulate manganese into nodules at the bottom of non-depositional zones.

# Physiological Ecology of *Mougeotia* (Zygnemataceae) from an Experimentally Acidified Lake

**Arancibia-Avila, P.E. 1994**
**University of Wisconsin at Madison, 153 pp.**

Filamentous green algae collected in July, 1989, from metaphytic blooms that occurred in the acidified (pH 5.2) basin, but not an unacidified reference basin (pH 6.1) of Little Rock Lake, Vilas Co., WI. Isolates of a *Mougeotia* species, the dominant bloom former, and *Spirogyra reflexa* were cultured in SD11 medium at pH 5.5, with aeration. Measurements of $O_2$ production in a factorial experiment revealed that optimal irradiance and temperature for photosynthesis in *Mougeotia* were 2500 $\mu E\ m^{-2}\ sec^{-1}$ and 25°C. Additional $O_2$ evolution measurements showed that the optimal pH for *Mougeotia* photosynthesis was 8, but that the net photosynthesis was positive from pH 8 to 3.

Further photosynthesis studies indicated that *Mougeotia* was tolerant to concentrations of zinc and aluminum that were greater than levels observed in the acidified basin of the lake. Since inorganic carbon ($C_i$) is known to limit *Mougeotia* photosynthesis and growth in acidified lakes, the occurrence of carbonic anhydrase (CA) as a mechanism for uptake and concentration of $C_i$ was investigated. No CA activity was detected in *S. reflexa.* In contrast, both external and internal CA were measured in *Mougeotia* at pH 3.7 and at pH 8, by means of a potentiometric assay. By comparison to pH 8, at pH 3.7 external CA activity increased by a factor of about 2.

An antibody to *Chlamydomonas* external CA was used to localize CA in the plasma membrane and cell wall of both *Chlamydomonas* and *Mougeotia.* A histochemical procedure that localizes CA in animal tissues gave positive results for pig liver, but did not work in any of the algae tested, possibly indication of differences in amount of enzyme activity between animal and algal CAs.

Finally, when unareated (DIC-limited) *Mougeotia* was grown in SD11 medium supplemented with 1% glucose, chlorophyll a levels were significantly higher than for cultures grown without sugar. Chloroplast morphology was also judged superior for sugar-supplemented cultures. The data suggest that *Mougeotia* possesses a DIC-concentrating system, and may also be able to import DOC (glucose).

# Extracellular Release and Sinking as Fates of Planktonic Primary Production: Variation along Productivity Gradients and between Lakes and the Ocean

**Baines, S.B. 1993**
**Yale University, 284 pp.**

The fate of organic matter produced by phytoplankton constrains the response of algal production and biomass to nutrient inputs, influences food web structure, and determines the export of nutrients, contaminants and organic matter from the euphotic zone to sediments. Two potentially important fates of phytoplankton production, the extracellular release of organic carbon (ER) and the sinking loss from the euphotic zone, were compared between marine and freshwater planktonic ecosystems of varying productivity.

Published ER estimates were most closely related to primary productivity and not algal biomass. This pattern does not support the notion that extracellular products diffuse passively from algal cells in natural systems. Differences exist between lakes and marine environments. In marine and estuarine ecosystems, ER averaged 12% and did not vary systematically along a trophic gradient. In lakes, ER was non-linearly related to productivity, averaging about 30% of primary production in oligotrophic lakes and 5% in eutrophic lakes. A comparison of regression models implies that dissolved organic material released by phytoplankton can support less than 50% of bacterial production in natural ecosytems.

Sinking fluxes of carbon, nitrogen, phosphorus and pigments were closely related ($r^2$=0.87-0.92) to metalimnetic pigments in lakes. Sinking velocities of particle communities are not systematically related to chlorophyll concentration. Since the amount of production per unit chlorophyll increases with productivity in lakes, a negative relationship between primary productivity and the percent of production lost to sinking (export ratio) was inferred and then validated by literature data. This pattern is opposite to that previously expected for lakes and that observed for the ocean. However, it is consistent with models relating chlorophyll concentration to primary productivity, sinking fluxes of carbon, and light attenuation in lakes and the ocean.

The difference between marine and freshwater export ratio-productivity relationships appears to stem from 12-fold lower production per unit chlorophyll in oligotrophic lakes than in ocean regions of similar chlorophyll concentrations. Particle community sinking velocities are also average 2- to 3-fold higher in the ocean. These discrepancies between marine and freshwater ecosystems indicate fundamental differences in the way planktonic communities process organic matter.

# Ecological and Evolutionary Consequences of the Caudal Spine in the Cercopagidae (Crustacea, Branchiopoda)

**Barnhisel, D.R. 1994**
**Michigan Technological University, 166 pp.**

Field analyses, direct/indirect interaction modeling, and functional response theory illustrate that the carnivorous crustacean, *Bythotrephes* (Onychopoda, Branchiopoda), is not a palatable prey for young fish < 100 mm due to its long caudal spine, but can potentially affect the foraging behavior of fish that compete with *Bythotrephes* for the zooplankton resource. Field analyses support predictions that *Bythotrephes* is not a preferred prey item for young fish, that there is a threshold size of fish which can utilize the spined zooplankter as a food source, and that fish are more likely to consume *Bythotrephes* as fish increase in size.

In terms of foodweb pathways, important interactions among fish, *Bythotrephes*, and the shared resource depend on how effective the predators are in consuming the resource. Alternative prey modeling and functional response theory indicates that *Bythotrephes* decreases the efficiency with which planktivorous fish forage on more palatable prey. Due to the extreme length of the caudal spine, *Bythotrephes* is difficult to ingest and fish must be able to discriminate it from other prey.

The frequency of *Bythotrephes* and absolute density of palatable prey must reach a certain threshold before fish are able to forage selectively. To determine whether the spine has lengthened over time because it confers additional fitness, a phylogeny of the Onychopoda can indicate whether the spine is a derived feature.

I conducted a comparative morphological analysis of the Onychopoda and proposed a molecular analysis to reconstruct onychopod phylogeny. Morphological features indicate that *Bythotrephes* consists of a single genus with a high degree of morphological variability and that it may not be as closely related to other onychopods as previously believed. Possible origins of onychopods and their relatedness to other branchiopods are discussed.

# The Effect of Dissolved Natural Organics on the Chronic Toxicity of Cadmium to *Mysidopsis Bahia* Molenock (Crustacea: Mysidacea)

**Bittner, M.A. 1994**
**George Mason University, 209 pp.**

Naturally occurring dissolved organic matter from two sites of the mesohaline area (salinity 12-14 ppt) of the Chesapeake Bay were used to determine the binding abilities for cadmium. The samples were found to contain two functional organic ligands as determined by cadmium titration, using an ion-selective electrode.

This method involves concentrating and desalting the natural ligands by ultrafiltration, followed by removal of metals bound to natural organics by cation exchange. The complexing ability of the two types of ligands was estimated by the two-component Scatchard function. The concentration of the stronger ligand ($L_1$) was determined to be in the range of 0.036-0.137 µM with a conditional stability constant (log $K_1$) of 5.12-5.83. The concentration of the weaker ligand ($L_2$) was estimated to be in the range of 2.49-15.30 µM, with a conditional stability constant (log $K_2$) of 2.99-3.20. It was found that almost 99% of the ability of dissolved organic matter to form complexes with cadmium in these estuarine samples is attributed to the weaker ligand.

To determine how the degree of cadmium complexation with natural organics affect the chronic toxicity of this metal to *Mysidopsis bahia*, the natural organic matter present in the estuarine samples was varied over a range of cadmium concentrations. Seven-day chronic toxicity tests were carried out with photooxidized (organic-free), non-photooxidized, and an equal mixture of photooxidized/non-photooxidized estuarine waters. Cadmium has significant effects on the survival, growth and fecundity of *M. bahia* ($P \leq 0.05$) without contributing effects from the organic matter concentration of the water. The interaction of cadmium and natural organics was not significant on any of the end points. Chronic values (ChV) for survival ranged from 6.6 to 12.3 µg/l, with a no observed effect concentration (NOEC) ranging from 4.3 to 10 µg/l. Both growth and reproduction showed greater sensitivity than survival in the presence of increasing cadmium concentrations. ChV for growth ranged from ≤3.5 to 5.1 µg/l, and from ≤3.5 to 5.1 µg/l for reproduction in all experiments. Seven-day $LC_1$, often used as an estimate of the threshold concentration, ranged from 3 to 6 µg/l. These results suggest that natural organic matter at the concentrations present in the estuarine samples (<3 mg/l) was not a determining factor for cadmium chronic toxicity. Cadmium speciation and complexation with constituents in the toxicity test sample water was calculated using the geochemical speciation model MINTEQA2. Simulations were performed using both stability constants from the thermodynamic data set included in MINTEQA2 and those determined in the present study. There was little difference between these stability constants. In these samples dissolved organic matter played a negligible role in determining the chemical form of cadmium, whereas chloride concentration, as determined by salinity, was the main factor controlling speciation. Therefore, in estuarine waters cadmium toxicity to *M. bahia* may be predictable directly from geochemical speciation of a system controlled by inorganic ligands.

# On the Seasonal Dynamics of *Daphnia* Species in a Shallow Eutrophic Lake

**Boersma, M. 1994**
**University of Amsterdam (Netherlands), 159 pp.**

The seasonal dynamics of crustacean zooplankton has been a topic of research ever since the end of last century. Three major factors influencing the dynamics of the zooplankton have received considerable attention in literature: temperature, food availability and predation pressure.

The seasonal dynamics of *Daphnia* species in Tjeukemeer, a shallow eutrophic lake in the Netherlands, were studied in order to infer the relative importance of the different steering factors in the seasonal dynamics of cladoceran freshwater zooplankton. As the temperature is relatively constant during the growing season research was focused on the effects of food and predators. In Tjeukemeer, two *Daphnia* species co-occur, *Daphnia galeata* and *D. cucullata*. Recent insights have shown that also the hybrid between these species occurs in large numbers in the lake.

Predation by different fish species was investigated by comparing the production of the Young-of-the-Year fish, the main zooplanktivores in the lake, with the mortality of the daphnids. From this it was concluded that the effect of fish is only profound in the second half of the growing season, when all mortality in the susceptible size classes could be explained by the predation of juvenile fish. In the first part of the growing season, when the numbers of the daphnids decrease dramatically during the summer decline, the predation by fish is not severe enough to explain this large mortality. Laboratory experiments showed that both growth and reproduction of animals of the genus *Daphnia* were influenced by both the quantity and the quality of the food. With the help of a detailed analysis of the condition of daphnids in the lake the degree of food limitation for the animals in the lake was determined. The condition of the animals was determined by measuring the length dependent carbon content. From this analysis it could be concluded that daphnids in Tjeukemeer are food limited during the largest part of the year, which leads to the conclusion that competition for limiting resources is also potentially important. Further analysis showed that indeed both parental species compete for resources with the hybrid, but that resource competition between the parental species seemed limited. A model analysis of this system showed that as a result of these competitive relationships no stable equilibrium exists with all three *Daphnia* taxa present, but that either the two parental species outcompete the hybrid, or the hybrid is the only taxon present in Tjeukemeer. The fact that still all three species co-occur shows that the environmental conditions in Tjeukemeer are far from stable.

## Delineation of the Hydrodynamics of Lake Michigan and Lake Baikal Using Satellite-Derived Surface Temperatures

**Bolgrien, D.W. 1993**
**University of Wisconsin at Milwaukee, 170 pp.**

The hydrodynamics of Lake Michigan and Lake Baikal were delineated using surface temperatures (SST) derived from the Advanced Very High Resolution Radiometer (AVHRR) aboard NOAA satellites. Lake Michigan data were obtained through the NOAA CoastWatch Program from May 1990 to July 1993. Images of Lake Baikal were collected between June 1990 and September 1991. AVHRR SST data showed the spatial and temporal dynamics of seasonal temperature cycles, thermal fronts, upwelling, and the interaction between the lakes and their bays and tributaries.

Thermal fronts in southern Lake Michigan typically formed in early May, but in 1991 fronts were first observed in mid-April. Fronts remained 5-30 km offshore for several weeks before rapidly migrating northward. By early June, water at temperatures <4°C was isolated in the northern basin. In 1992 and 1993, the northward migration was briefly reversed as the 5°C isotherm moved south before resuming its northward progression. The influence of the Grand and Milwaukee Rivers on spring warming was not observed in SST images. Water exchange between Green Bay and Lake Michigan occurred through the Sturgeon Bay Canal and at the mouth of the bay. Extensive upwelling was also observed in this area along the Door Peninsula.

The range of SST in the lake was small in winter and summer indicating relatively uniform thermal conditions as compared to spring and fall when temperatures rapidly responded to seasonal change. The maximum whole-lake median SST in 1991 was 23.8°C which was >4°C higher than in the other years studied. Minimum median SST ranged from 2.5°C in 1991 to 4.2°C in 1993.

Lake Baikal was ice-free in early June. The Selenga, Barguzin, and Upper Angara Rivers were significant sources of heat to the surface waters. The southern and middle basin warmed more quickly than the northern basin, however, the relatively shallow northern basin reached higher summer temperatures of about 16°C. Thermal fronts were generally associated with topographic features such as sills, coastal wetlands, bays, and river deltas. Upwelling in Lake Baikal was not clearly depicted using AVHRR SST data. Bands of relatively warm water persisted near shore throughout the lake in summer.

AVHRR SST provide a means of linking thermal structures, hydrodynamics, and biogeochemical processes in large lakes. Systematic changes in thermal structures may serve as indicators of regional or global climate change.

# Distribution Patterns of Coccolithophorid Blooms and their Biogeochemical Significance

**Brown, C.W. 1993**
**University of Rhode Island, 278 pp.**

Coccolithophorids are an abundant and widely distributed component of the marine phytoplankton that are thought to play an important role in the oceanic carbon and sulfur cycles through their production of coccoliths, composed of calcium carbonate, and dimethyl sulfide (DMS). The biogeochemical influence of coccolithophorids is probably most pronounced when they occur in "bloom" proportion. Yet little is known of how prevalent these blooms are in the ocean.

To ascertain the prevalence of coccolithophorid blooms and estimate their $CaCO_3$ and DMS production on a regional and global scale, their distribution pattern was mapped in the western North Atlantic and the global ocean. Mapping was accomplished by classifying pixels of coastal zone color scanner imagery into bloom and nonbloom classes based on their mean normalized water-leaving radiances using a supervised, multispectral scheme. Coccolithophorid blooms can be distinguished from most other water conditions in visible satellite imagery because of their unique spectral signature characterized by high water-leaving radiance at all visible wavelengths.

In the western North Atlantic, surface waters with the spectral signature of coccolithophorid blooms annually covered an average of 300,000 $km^2$ in the Gulf of Maine, the Gulf of St. Lawrence and on the Nova Scotian Shelf and Slope, the Grand Bank and the shelf off northeastern Newfoundland and southeastern Labrador.

Globally, surface waters with the spectral signature of coccolithophorid blooms annually covered an average of $1.4 \times 10^6$ $km^2$ in the world oceans from 1979 to 1985, with the subpolar latitudes - particularly the North Atlantic - accounting for 71% of this surface area. The blooms were most extensive in the subarctic North Atlantic. Large expanses of the bloom signal were also detected in numerous lower latitude marginal seas, though the condition(s) responsible for this signal is equivocal. The greatest spatial extent of classified blooms in subpolar oceanic regions occurred in the months of summer - early autumn, while those in lower latitude marginal seas occurred in mid winter - early spring.

Classified blooms are presumed to be composed primarily of the coccolithophorid *Emiliania huxleyi* (Lohmann) Hay et Mohler. This presumption was substantiated in the western North Atlantic by noting the presence of *E. huxleyi* coccospheres and/or detached coccoliths at high concentrations in or near the vicinity of high reflectance patches observed in contemporaneous visible AVHRR (Advanced Very High Resolution Radiometer) imagery. However, the presence of conditions that could mimic the spectral characteristics of coccolithophorid blooms renders the determination of actual bloom presence equivocal in some geographic areas, particularly on shelf regions at lower latitudes.

Standing stock estimates suggest that the presumed *Emiliani huxleyi* (Lohmann) Hay et Mohler blooms act as a significant source of calcite carbon and DMS sulfur on a regional basis. On a global scale, however, satellite-detected coccolithophorid blooms are estimated to play only a minor role in the annual flux of calcite and DMS from the surface mixed layer to depth and the atmosphere, respectively.

## Sedimentation Processes in Selected Coastal Wetlands from the Gulf of Mexico and Northern Europe

**Callaway, J.C. 1994**
**Louisiana State University, 223 pp.**

Sediment cores were collected from coastal wetlands from the Gulf coast of North America and northern Europe to study accretion rates and heavy metal accumulation. There was a significant decrease in vertical accretion rates from low to high marsh for Gulf coast samples. Contrary to previous results, these low-tidal-range sites did not have negative accretion balances. Northern European samples demonstrated the utility of Chernobyl $^{137}Cs$ as a sediment marker. There were large differences in sediment characteristics and accretion rates between Polish and western European samples. Vertical accretion rates based on $^{210}Pb$ were lower than $^{137}Cs$ rates for most cores. The $^{210}Pb$ rates included effects of compaction and decomposition, and profiles of bulk density and organic content confirmed this. All European sites had positive accretion balances. Multiple regression analyses of a large data set showed that vertical accretion rates were best described by a regression using relative sea level rise, surface organic content, sediment bulk density, position within the marsh, and the interaction between relative sea level rise and position. The significance of the interaction term indicated that low marsh sites responded differently to increases in relative sea level rise than middle and high marsh sites. There was a much higher correlation between vertical accretion and organic accumulation than between vertical accretion and mineral accumulation. A computer model, using an annual cohort approach, successfully simulated sedimentation processes, including surface sediment deposition, below-ground production, decomposition, and compaction. Sensitivity analyses indicated that the most important factors affecting model-generated accretion rates were: pore space, mineral matter deposition, initial elevation, sea level rise, and below-ground production. Chronologies of sediment heavy metal concentrations for high and low marsh cores from northern Europe showed very good agreement, indicating that sediment profiles represent historic inputs of heavy metals. Some of the sediments had very high heavy-metal concentrations, with peak sediment concentrations up to five times greater than found in the oldest sediment samples. Metal concentrations have recently decreased in the cores from St. Annaland and Stiffkey Marshes but remained high throughout the upper part of the cores from the Oder River.

# Induction of the Sexual Phase and its Related Aspects in the Rotifer *Brachionus plicatilis*

**Carmona, M.J. 1992**
**University of Valencia (Spain), 266 pp.**

The present study on *Brachionus plicatilus* provides some new information on the biology of sexual reproduction in this species. It demonstrates the importance of density as inductive factor of mixis and the existence of intraspecific differences in the control of sexual reproduction. Furthermore, it helps to interpret the functional significance of density response in *B. plicatilis*. Finally, the study permits an approach to the analysis of the ecological significance of the evolution of stimuli for the transition from parthenogenetic to sexual reproduction.

The study is structured in two parts. In the first part, intraspecific variability due to both age and genotype in *B. plicatilis* is studied using a modified ultrasensitive silver-stain procedure to detect total proteins in polyacrilamide gels. Results from analysis of intraspecific genetic variability show a high level of interpopulational variation, contrasting with a low level of intrapopulational variation. Analysis of total-protein patterns related to age show the existence of age-dependent changes which permit the characterization of individual aging. Variability is great among isogenic individuals cultured in the same environment.

The aim of the second part, the main part of the study, is to determine the optimal timing of mixis in rotifer heterogenic cycles. This part focuses on the study of mixis induction, on related internal and external factors, and on implications of the sexual reproduction pattern in *B. plicatilis*. A dynamic model has been developed to theoretically address rotifer mixis. Results from simulations stress that the optimal timing for mixis is mainly related to the moment at which the habitat becomes unsuitable for population growth. Empirical results from the study manifest the effect of population density on mictic-female production and its modulation by both parental age and genotype. Experiments carried out to determine the density effect mode of action show that it may be attributed to the accumulation of some chemical substance released into the medium by the rotifers themselves. The detected unspecific chemical effect of crowding on mictic-female production in *B. plicatilis* suggests that the role of population density in mixis induction may be related to a strategy to escape through diapause from a deteriorating habitat. Finally, results from demographic and biochemical analysis show that sexual reproduction has important physiological implications: the aging process occurs earlier in mictic females than in amictic ones, probably as a result of differences in patterns of reproductive resource allocation between the two types of females.

# Demographic Consequences of Seasonal Variation in Environmental Stress

**Chen, C.Y. 1994**
**Dartmouth College, 174 pp.**

Environmental stressors, either naturally occuring or anthropogenically induced, are those biotic and abiotic conditions in which individuals exhibit declines in growth and reproduction and increases in mortality. Population level consequences of environmental stress, such as declines in population growth rates and abundances, are determined by species-specific responses to the environmental conditions as well as the phenology and life history characteristics of specific populations in the field. This thesis examines the effects of biotic (food quality) and abiotic (temperature) sources of environmental stress on zooplankton populations.

Zooplankton experience great variability in the types and quantities of foods available during their lives and the presence of poor quality foods can be detrimental to those individuals feeding on them. Measurement of both short term feeding rates and long term demographic parameters of the calanoid copepods, *Diaptomus minutus* and *Epischura lacustris*, were made when individuals were offered two edible algal foods, *Cryptomonas erosa* and *Chlamydomonas reinhardi*. Experiments in which animals were fed differing quality foods showed that ingestion rate was inversely correlated with food quality. In addition, ingestion rates and biochemical measures of food quality were not reliable predictors of the effects of food quality on demographic parameters. Assimilation rates appeared to be the best short term predictor of longer term parameters such as survival and reproduction.

Temperature changes in the field also may be a source of stress to aquatic organisms if temperatures exceed their tolerance ranges and limit growth rates and reproduction. The effects of seasonal temperature variation on demographic and life history characteristics of two co-occuring zooplankton species, the calanoid copepod, *E. lacustris*, and the cladoceran, *Daphnia catawba*, were measured and compared in a combined laboratory and field study. Field measurements including ambient lake temperature, zooplankton abundance, and egg production were made during the ice-free season in Norford Lake, Thetford, Vt. Laboratory experiments were conducted in the late spring and fall to measure survival and reproduction over a natural range of temperatures (15° 20° 25°, and 30°C) and in different rates of temperature change. In Norford Lake, ambient lake temperatures changed rapidly and increased above 30°C in mid-summer. *E. lacustris* and *D. catawba* showed similarities in their seasonal phenologies but differences in their thermal tolerances. Seasonal reproduction of *E. lacustris* in the field was negatively correlated with ambient lake temperature and *E. lacustris* adults exhibited declining performance with increasing temperatures above 15°C. In contrast, *D. catawba* juveniles and adults did not experience thermal stress at temperatures below 30°C. Neither species showed an ability to acclimate to warm stressful temperatures in the short term, and the overwintering strategies of both species appeared to be altered by temperature increases in the fall.

Finally, temperature often has been overlooked as an important mechanism for structuring zooplankton communities or seasonal succession. This omission occurs even though temperature is known to affect individual or population performance The last part of this study compares the effect of temperature on the seasonal demographic patterns of *E. lacustris* and *D. catawba*. The thermal responses of these two species appear to provide an explanation for the timing of their peak abundances in the field. In addition, an understanding their species-specific thermal reponses, life history strategies, and seasonal phenologies provide insights into the potential consequences of seasonal warming events for populations of each species in the field.

# The Fluorescence of Dissolved Organic Matter in the Marine Environment

**Chen, R.F. 1992**
**University of California, San Diego, 149 pp.**

Dissolved organic carbon (DOC) is a major pool of reactive carbon that must be considered in the global carbon cycle. Unlike dissolved inorganic carbon and atmospheric $CO_2$, DOC is composed of perhaps millions of distinct organic molecules, each with a different reactivity. DOC must be considered as a mixture of several fractions of molecular types with different residence times and geochemical cycles in order to understand DOC cycling.

It has been known for over four decades that dissolved organic matter in seawater emits a blue fluorescence when irradiated by ultraviolet light. Due to the spatial and temporal uniformity of the fluorescence spectrum, variations in fluorescence intensity (Ex l = 325 nm, Em l = 450 nm) can be related to variations in the concentration of the "fluorescent fraction" of DOM rather than compositional or environmental changes. Very sensitive laser-induced fluorescence measurements at 28 stations in the Atlantic and Pacific Oceans reveal the global cycle of the fluorescent fraction of DOM. In all cases, surface seawater fluorescence is low due to photochemical bleaching which occurs on the timescale of hours. Fluorescence of deep water is 2 to 2.5 times higher than in surface waters and is generally constant, increasing only 25 % from the Atlantic to the Pacific suggesting a long residence time of ~2000 to 4000 years for fluorescent organic matter. In mid-depth open ocean waters (100 to 1000 m), fluorescence and nutrients (nitrate and phosphate) correlate very well suggesting that formation or regeneration of fluorescent materials accompanies the remineralization of settling organic particles.

Fluorescence of dissolved organic matter in porewaters reveals some important processes of early diagenesis and consumes very little sample. Data from six areas agrees with a model in which labile organic matter is broken down to low molecular weight monomers and are thus either remineralized to $CO_2$ or polymerize to form "humic substances" that are ultimately buried in the sediment. Fluorescence represents these high molecular weight polymers and increases downcore with increases in alkalinity, ammonium ion, and phosphate in anoxic sediments. Fluorescence thus represents the majority of the DOC in porewaters and therefore can be used as a first order estimate of DOC. In the Santa Barbara Basin, seawater fluorescence and DOC increases near the bottom and large enrichments in the porewaters suggests that dissolved fluorescent organic material is diffusing out of sediments and into overlying waters, thus having a significant local impact on the DOC cycle.

The fluorescent fraction of DOM can be described as "humic substances" and can further be broken down into several components using high performance liquid chromatography. A method has been developed to examine porewaters and fluorescent material extracted from ~ 1 l of seawater by solid phase extraction (Sep-Pak $C_{18}$). Most samples reveal three or four sharp peaks, one or two polar components and one or two hydrophobic components. Seawater extractions and surface porewaters are generally the same compositionally, but there are variations due to hydrothermally generated organics such as in Guaymas Basin surface sediments and near the decollement in the Nankai trench ~965 mbsf. Changes in the retention times and peak areas represent diagenetic patterns in sediment cores and can be used in conjunction with other information to understand compositional changes in DOC.

# Variability of Water Quality Data Collected Near Three Major Southern California Sewage Outfalls

**Conversi, A. 1992**
**University of California at San Diego, 110 pp.**

As human impacts on the ocean have largely increased in the last century, a question of primary interest now facing scientists is whether changes in environmental variables can be attributed to human input or are simply natural. Answering this question is crucial in assessing human impact on the environment, yet is complicated by the fact that the natural variability of oceanic properties is very high and still largely undefined.

Currently about 4500 million liters of treated sewage effluent are discharged daily in the Southern California Bight, mostly through three major submarine outfalls, a freshwater input greater than the natural input from rivers, runoff and storms in the region. It is however unclear whether these artificial rivers are affecting the water column physical properties and biology. This research investigates the relation between variations in "anthropogenic" properties, i.e. properties input by humans in the ocean (sewage flow and suspended solid discharge), and water column properties (Secchi depth transparency, percent transmissivity, temperature and dissolved oxygen) measured near three sewage discharge sites in the Southern California Bight: the Santa Monica Bay outfall of the city of Los Angeles; the Palos Verdes Peninsula outfall of Los Angeles County; and Point Loma outfall of the city of San Diego. Data on the same variables had been collected for 15 years at control and test locations with comparable methods in all three areas.

Time-series analyses were used to investigate the variability of both anthropological and water column properties at the three locations (50-200 km apart). Comparisons among the areas and correlations with the sewage discharge within each area were used to distinguish the natural from anthropogenic sources of variability. In fact, previous studies have shown that many physical and biological water column variables (including temperature, zooplankton biomass and phytoplankton abundance) are coherent at interannual and annual frequency bands over the entire Southern California Bight. In other words, they tend to rise and fall simultaneously from year to year. The question was: Does the same happen also in areas with a large anthropogenic input?

My analysis of the sewage inputs showed that the three discharges were not coherent in any frequency band. Thus, coherence in the water column across the Bight would indicate a Bight-wide (natural) driving force, while correlations with the local discharges would indicate anthropogenic driving force.

The analysises of the water column variables showed no correlations between any water column properties and the sewage properties. Morevover, the interannual components of transparency, transmissivity and (particularly) temperature were correlated, within each area, between test and control stations, and were also correlated across areas. Thus, the dominant mode of the fluctuations of these three properties was natural (Bight driven) rather than driven by the local anthropogenic discharges. On the other hand, oxygen did not show common temporal patterns even between the stations within the same area, thus cross-Bight comparisons of this property could not be made.

# The History of Diatom Community Structure, Eutrophication and Anoxia in the Chesapeake Bay as Documented in the Stratigraphic Record

**Cooper, S.R. 1993**
**Johns Hopkins University, 302 pp.**

Ongoing monitoring programs and historical data are not sufficient to establish anthropogenic effects on the water quality and ecology of Chesapeake Bay. However, stratigraphic records preserved in the sediments of the mesohaline Chesapeake Bay were used to reconstruct a 2,000 year history of sedimentation, eutrophication, anoxia and diatom community structure from pre-Columbian to modern times. Diatoms, pollen, total and organic carbon (TOC), total and organic nitrogen, total sulfur, acid-soluble iron, an estimate of the degree of pyritization of iron (DOP), and biogenic silica (BSi) were used as paleoecological indicators in four sediment cores collected in a transect across the Chesapeake Bay from the Choptank River to Plum Point, Maryland. Surface salinities in this area of the Bay average 8-15‰.

The four gravity cores (114-160 cm long) were collected in areas that currently experience different patterns of hypoxic and anoxic bottom waters. The sediments within the cores were dated using radiocarbon and pollen techniques. The $^{14}C$-determined dates at the bottom of the cores range from 910-2650 years before present. Sedimentation rates were determined (0.2-5.8 mm $yr^{-1}$) using pollen methods, and a chronology for each core was compiled. Geochemical indicators were measured and diatom species identified and counted at subsampled 2 cm intervals within each core. More than 400 diatom species, primarily marine and estuarine taxa, were identified in the sediments of the Chesapeake Bay, some for the first time. The taxonomy, autecology, and observed valve morphology of the 50 most abundant species are discussed.

Analysis of the data indicates that sedimentation rates, eutrophication, turbidity, and anoxia have increased in the mesohaline Chesapeake Bay since the time of European settlement of the watershed and land clearance for agriculture. There is also evidence that freshwater input to this area of the Bay has increased. Changes in diatom community structure and geochemical indicators reflect major changes in land use patterns of the watershed. Large increases in organic carbon and nitrogen seen in the sediment samples, as a function of time, cannot be readily modeled using accepted decay models for reduction in marine sediments. Several DOP measurements dated post-1900 indicate restricted bottom water oxygen conditions in this area of the Chesapeake Bay. Diatom community diversity exhibits a continuing decline since about 1760 A.D., while centric/pennate ratios rise dramatically in most recent sediments. Diatom communities from samples of all four cores dated within similar time periods of land use are shown to be clustered together by the unweighted pair group method using arithmetic averages (UPGMA) of Euclidean distance measures between samples.

# The Biogeochemical Cycling of Methane in the Upper Ocean off Southern California

**Cynar, F.J. 1992**
**University of California at San Diego, 235 pp.**

Interdisciplinary research into the physical oceanographic, microbiological, and geochemical processes maintaining the supersaturation of methane in the surface ocean was carried out off southern and central California ($1.9 \times 10^5$ km$^2$ area between 30° and 35.5°N). Data were obtained in the laboratory and at sea during twelve cruises over a period of 37 months. The supersaturation of methane in southern California waters (maximum $>10^3$ nM) and its variability across space and time were consistent with the proximity of hydrocarbon seeps in regions of physical mixing and stirring. *In situ* microbiological production of $CH_4$ associated with net plankton was also observed and led to the first description of the enrichment, identification, and characterization of a marine methanogenic bacterium (kingdom Euryarchaeota: serologically typed to *Methanococcoides methylutens*) from the surface waters of the ocean. *In vitro* rates of methanogen doubling and $CH_4$ production suggested that *in situ* methanogenesis may be a significant source of water column methane. The inherent uncertainties associated with extrapolating *in vitro* studies to natural waters, however, restricts their importance. A descriptive analysis of the observed variations in the concentration of $CH_4$ over the temporal and spatial scales of this investigation, suggested that processes of a biological or physical nature were operating along localized isopycnals. A model of the distribution of $CH_4$ in the upper water column showed that horizontal advection of seep-derived methane from the coast and the subsequent eddy diffusion across select isopycnal surfaces provided a satisfactory fit to the data. The dominant influence of physical oceanographic processes was further evidenced from analysis of three dimensional methane and hydrographic data that showed relatively high inventories of $CH_4$ off Point Conception (34.5°N) were correlated with intensified upwelling phenomena, and anomalous patches of elevated $CH_4$ were associated with offshore eddies of the prevailing California Current.

The flux of $CH_4$ to the atmosphere was characterized on several spatial and temporal scales. Estimates of the dominant methane sink provided an important, although uncertain, term for exploring subsequent mass-balance considerations of the biogeochemical system. At the vertical scale of the ocean's mixed layer, a steady-state consideration of >100 vertical methane profiles together with corresponding sea-air flux estimates suggested that the concentration of $CH_4$ in the mixed layer may be modeled simply as the balance between two physical processes: (1) the vertical eddy diffusive flux from the methanocline (located at the bottom of the mixed layer) and (2) the diffusive flux across the sea surface. At the horizontal scale of the Southern California Bight, estimates of the mass of $CH_4$ vented to the atmosphere and estimates of the potential mass of methane transferred by the long-term mean Ekman transport of water away from the southern California coast, were concordant. At the planetary scale, extrapolation of the 1989-90 annual sea-air flux estimate for southern California (37 mg $CH_4$ m$^{-2}$ yr$^{-1}$) to the global area of coastal waters, suggests that coastal waters may account for 25% of current estimates of the total oceanic input of $CH_4$ to the atmosphere.

# Detection of Optical Water Quality Parameters for Eutrophic Waters by High-Resolution Remote Sensing

**Dekker, A.G. 1993**
**Vrije University (Netherlands), 222 pp.**

This research focussed on understanding the relationship between water quality parameters, the inherent optical properties, and the subsurface irradiance reflectance, for application in remote sensing. The multitemporal and multi- sensor applicability of the derived algorithms has been demonstrated by the successful application to remote sensing data from two instruments, flown on two days under different conditions. The strength of this approach lies in the ability for combining information and results from underwater light climate research as well as in situ and remote sensing reflectance measurements.

Improvements are possible if more information concerning the scattering and backscattering (and, therefore, volume scattering functions) of the phytoplankton and the tripton was available. Therefore a decrease in analytical and an increase in semi-empirical elements in the algorithms were required, in successive order, for chlorophyll *a*, cyanophycocyanin (CP-cyanin), seston dry weight (DW), vertical attenuation coefficient for downwelling irradiance ($K_d$), and Secchi disk transparency (SD). Chlorophyll *a*, CP-cyanin and seston are parameters that influence the optical characteristics of water, whereas $K_d$ and SD are a function of the optical properties of the water.

The large range in optical water quality parameters in the study area has led to new insights: the variability in specific absorption and scattering coefficients within and between the four different water types indicates that the development of remote sensing algorithms for inland water quality analysis must reckon with adjustable parameterisation of absorption and scattering variables for each water type studied.

The subsurface irradiance reflectance, R(0-), is the essential parameter for applications of the analytical model for remote sensing. It is essential because R(0-) can be determined from the inherent optical properties of a (absorption coef.), b (scattering coef.) and $B(\theta)$ (volume-scattering function, where $\theta$ = angle of scattering), from in situ spectroradiometric measurements and from remote sensing measurements.

For chlorophyll *a* and CP-cyanin concentration estimation the analytical model provided the means to perform a sensitivity analysis on the influence of other parameters such as aquatic humus and tripton. Natural variations in aquatic humus and tripton levels in these waters led to 35 $\mu g\ l^{-1}$ and 10 $\mu g\ l^{-1}$ chlorophyll *a* equivalent error respectively. This indicates that estimates of the other inherent optical properties are required for successful application of these algorithms.

From the combined absorption and scattering coefficients of all parameters it was deduced that for remote sensing the spectral areas where only one dominant spectral feature is present will be the most useful for determining inland water quality. Such features include the 624 nm CP-cyanin and the 676 nm chlorophyll *a* absorption features and the overall absorption minimum at 700 - 710 nm. Below 500 nm the effects of absorption by aquatic humus, phytoplankton and tripton and the high level of scattering are compounded, presenting a four-parameter equation of influence on the reflectance signal measured by remote sensing.

# Long-Term Monitoring of Reef Corals at the Flower Garden Banks (Northwest Gulf of Mexico): Reef Coral Population Changes and Historical Incorporation of Barium in *Montastrea Annularis*

**Deslarzes, K.J.P. 1992**
**Texas A&M University, 170 pp.**

Reef coral populations were monitored from 1988 to 1991 at the Flower Garden Banks located in the northwestern Gulf of Mexico. The status of reef coral populations, and natural or man-made factors potentially affecting their well being were determined. Man-made chronic disturbances are degrading coral reef resources on a global scale. Yet, the Flower Garden coral reefs seem to have been widely sheltered from the effects of regional stresses generated by population growth and increased industrial activity.

Since 1974, reef coral population levels have remained unchanged in the *Montastrea-Diploria* Zones at the Flower Garden Banks. Live coral cover ranges between 46 and 46.5 %. *Montastrea annularis* and *Diploria strigosa* comprise 80% of the coral cover on either bank. The remainder of the cover is mostly sharedby eight other taxa even though 12 hermatypic coral species inhabit the *Montastrea-Diploria* Zones. *P. astreoides*, *M. annularis*, *Agaricia* spp. and *Diploria strigosa* are the most abundant species (> 80 % of colony counts).

Coral taxa appear to be more homogeneously distributed on the West Bank. The relatively greater number of *Agaricia* spp., *Madracis decactis*, and *P. astreoides* colonies on the East Bank may be the source of a decreased evenness. The health of reef corals was assessed using repetitive and non-repetitive photographic methods, and accretionary growth measurements of *M. annularis*. Reef corals have undergone small scale changes at the Flower Gardens probably reflecting natural disturbance, predation, disease, and inter-specific competition. More tissue was gained than lost in repetitive photographic quadrats. The causes to most of the tissue loss were unknown. White mat disease (ridge disease) is shown to generate more tissue loss than any of the three bleaching events that took place at the Flower Gardens (1989, 1990, and 1991). Advance to retreat linear ratios of encrusting growth revealed a net tissue gain on the East Bank and a net tissue loss on the West Bank. In situ and retrospective accretionary growth rates of *M. annularis* were highly variable. Retrospective growth rates (5.3 and 7.8 mm/yr) were estimated using a new method. The mean in situ growth rate was 4 mm/6 mo 13 S.D. The annual barium content from 1910 to 1989 in a *M. annularis* colony from the West Flower Garden did not reveal trends associated with the extensive oil and gas exploration in the northern Gulf of Mexico.

# Nitrogen Dynamics in a Coastal Upwelling Regime

**Dickson, M.-L. 1994**
**Oregon State University, 227 pp.**

In an effort to expand our knowledge of the environmental factors regulating nitrogen utilization in a coastal upwelling system, thirteen experiments were undertaken at a site off the Oregon coast. The sampling entailed measuring ambient biomass and nutrient concentrations, primary production rates using $^{15}N$ (i.e. nitrate, ammonium and urea) and $^{14}C$ tracers, and ammonium regeneration rates at six depths over two upwelling seasons and one winter.

A comparison of PN-specific, absolute and Chl *a*-specific nitrate uptake rates was undertaken to assess to if temporal changes observed in uptake rates were due to the phytoplankton metabollically adapting to the upwelling environment or were due to variations in phytoplankton biomass.Although PN-specific and absolute uptake rates showed no dependence on the nitrate concentration, Michaelis-Menten kinetics were found to apply when the uptake rates were normalized to Chl *a*. Chl *a*-specific nitrate uptake rates were saturated when nitrate concentrations were greater than 5 μM. Uptake rates decreased in response to either low nitrate concentrations or when extremely high phytoplankton biomass caused shading. PN- and Chl *a*-specific uptake rates were similar when Chl *a* concentrations were ≥4 μg/liter and phytoplankton nitrogen comprised most of the PN pool. When Chl *a* was <4 μg/liter, however, phytoplankton nitrogen accounted for only 20-30% of the PN, and estimated phytoplankton-specific uptake was five-fold greater than PN-specific uptake rates.

Nitrate uptake rates were highest in the surface layer during the spring and summer months after upwelling events injected high concentrations of nitrate into the euphotic zone and a phytoplankton bloom had developed. High ammonium uptake rates were located 8 to 12 m below the surface and coincided with phytoplankton blooms and post-bloom conditions when upwelling had ceased. Urea concentrations and uptake rates were the lowest of the three nitrogenous nutrients studied. Urea uptake rates were highest during post-bloom events and exhibited light-dependent uptake kinetics like nitrate. Nitrate uptake comprised 55% of the nitrogen assimilated in this ecosystem, compared to 35% for ammonium and 10% for urea. Estimated annual rates of primary production are higher than previously reported for this region, although good agreement was obtained between $^{15}N$ (1400 $gC/m^2/y$) and $^{14}C$ (1900 $gC/m^2/y$) tracers.

In order to further assess the contribution of ammonium to phytoplankton nutrition, uptake and regeneration time course experiments were conducted. Both ammonium uptake and regeneration rates measured over 12 to 18 hours remained essentially constant. Unlike earlier studies, no evidence was found in support of time-dependent rates. However, as the length of the incubations increased the amount of usable data decreased dramatically due to key assumptions of the $^{15}N$ method being violated. Mass balance calculations indicated that 22 to 51% of the ammonium removed from the dissolved pool was not recovered in the particulate fraction. This appeared to be a more serious problem at 0 and 8 m (47%) than 25 m (22%). As a result, ammonium uptake rates were probably underestimated. At 0, 12, and 20 m uptake rates either balanced or exceeded regeneration rates, while at 8 and 25 m net regeneration occurred. Ammonium uptake rates were highest during the upwelling season (11 to 17 mmol $N/m^2/d$) and lowest during the winter (3 mmol $N/m^2/d$), whereas regeneration rates did not differ significantly between seasons (11 to 20 mmol $N/m^2/d$).

# Diatom Ecology and Paleolimnology of High Arctic Ponds

**Douglas, M.S.V. 1993**
**Queen's University (Canada), 161 pp.**

Epiphytic, epilithic, and surface sediment diatom assemblages were identified and enumerated from a suite of 35 study ponds from Cape Herschel (78°37'N, 74°42'W), east-central Ellesmere Island. Physical and chemical limnological data indicate that all the sites are shallow (maximum depth, $Z_{max}$ <2 m), clear, oligotrophic and freshwater. The ponds are completely frozen for 10 months of the year; however, during the short summers, water temperatures warm substantially (to a recorded maximum of 17°C) and fluctuate diurnally. With the exception of one pond (Paradise Pond, pH = 6.5), the ponds are alkaline (pH range of 7.4 to 8.60), reflecting local geology (e.g., calcareous tills). Major ions in water are relatively similar amongst the 35 sites, although environmental gradients exist.

Over 130 taxa from 28 genera were identified in the periphyton samples. Although some of the recorded taxa were common to all three habitats, many of the diatom taxa exhibited varying degrees of microhabitat specificity. Marked differences in species composition are evident amongst the ponds. Variance partitioning by CCA (Canonical Correspondence Analysis) showed that 26% of the total variance exhibited by diatom assemblages could be explained by the measured environmental variables (i.e., 10.2% by habitat and 15.8% by water chemistry). Further analyses of individual microhabitat assemblages identified alkalinity as the common environmental variable explaining a significant portion of the diatom data variance. Other important environmental variables were: [Na] and the percentage of moss and sediment within the pond for epilithic assemblages; and [$SiO_2$] for epiphytic assemblages. A DCA ordination of the three assemblages showed that sediment assemblages represented reasonable integrators of the various microhabitats, thereby reconfirming their usefulness for paleolimnological interpretations. Weighted averaging and calibration were used to develop a transfer function to infer pondwater alkalinity. Optima derived from rock and sediment assemblages were more reliable than those derived from moss assemblages.

Paleolimnological analyses from seven ponds showed that sediment cores from these shallow sites do appear to faithfully record a useful stratigraphic record of environmental change. The ponds' sediments span time frames ranging from about 9,000 years to a few centuries, depending on their proximity to the sea and the pattern of isostatic emergence. Striking successional changes were noted in diatom assemblages during the ponds' recent (ca. last 200 year) histories. In most sites, a long-lasting (several thousand year) and relatively stable benthic *Fragilaria pinnata/construens* assemblage was replaced by a diverse assemblage of benthic diatom taxa (e.g., *Achnanthes* spp., *Nitzschia* spp., *Cymbella* spp, *Pinnularia balfouriana*). Diatoms that apparently thrived on Cape Herschel a century or two ago (e.g., *Epithemia sorex*, *Fragilaria pinnata/ construens* complex etc.) no longer live on the Cape, further suggesting that this region has experienced recent environmental changes. Although the causes of these diatom assemblage shifts cannot be determined at this time, regional environmental changes likely related to anthropogenic activity may be responsible.

# Biological Consequences of Current-Topography Interactions at Cobb Seamount

**Dower, J.F. 1994**
**University of Victoria (Canada), 231 pp.**

Current-topography interactions at seamounts give rise to a variety of flow phenomena, the two most important being (i) the formation of Taylor cones, and (ii ) isopycnal doming. Since the 1950's the classical explanation for the high productivity of shallow seamounts has been that (i) upwelling over seamounts promotes enhanced primary production and that (ii) Taylor cones trap and concentrate this primary production. This theory further suggests that energy is transmitted to local zooplankton stocks which act as the food source supporting seamount fish populations. This thesis challenges the validity of this theory, based on sampling carried out at Cobb Seamount during 1990-92: isopycnal doming and Taylor cone recirculations *do* occur at Cobb, but the recirculation is too deep to trap plankton. Nevertheless, phytoplankton stocks *are* consistently high near Cobb, with local chlorophyll concentrations at least twice as high as background levels. The region of high chlorophyll concentration maps closely with regions of strong isopycnal doming and provides the first evidence that high phytoplankton stocks may be *permanent* features near shallow seamounts.

Spatial patterns in zooplankton community composition are also examined. Based on straight-line separation, community composition around Cobb changes only slightly over distances ≤150km. When samples are compared on the basis of relative distance to Cobb, however, it is seen that proximity to the seamount is a better predictor of community variability. Between-sample resemblance is *lower* among samples ≤30km from Cobb. This pattern may result from (i) predation by seamount fish or (ii) behaviour that causes zooplankton to avoid the seamount.

A simple ecosystem model is used to investigate (i) how high phytoplankton stocks are maintained over seamounts in the absence of trapping mechanisms, and (ii) whether seamount fish stocks rely on autochthonous energy sources. The model shows that persistent high phytoplankton stocks result from improved light conditions experienced by the phytoplankton as they dome over the seamount. The model also demonstrates that (i) the addition of nutrients to near-surface waters via doming may also be important and (ii) phytoplankton stocks are essentially unaffected by predation on zooplankton by seamount fish .

Together, the field data and the model show that while current-topography interactions *do* contribute to the maintenance of high-biomass communities at seamounts, the classical bottom-up enrichment/retention mechanism does not apply to Cobb. This work also suggests that seamount fish stocks rely on allochthonous energy sources. Rather than a long chain linking phytoplankton to zooplankton to fish, the "seamount effect" near Cobb results from an assortment of physical-biological interactions. Different organisms operating at several levels of the food web "feel" the influence of the seamount in different ways that are only loosely and occasionally coupled.

# Genetic and Evolutionary Consequences of Various Reproductive Strategies in the Sea Anemone Genus *Epiactis*

**Edmands, S. 1994**
**University of California at Santa Cruz, 187 pp.**

Four morphologically similar species in the sea anemone genus *Epiactis* live on the Pacific coast of North America: *E. prolifera*, *E. lisbethae*. *E. ritteri*, and *E. fernaldi*. All brood their offspring, but each has a different combination of internal vs. external brooding and hermaphroditism vs. gonochory (separate sexes). Studies were undertaken to determine mating systems, population genetic structures and phylogenetic relationships in these species.

Allozyme and multilocus DNA fingerprint analyses of the gynodioecious hermaphrodite *E. prolifera* show offspring are all identical to their mothers, suggesting that cross-fertilization is unlikely, but that either self-fertilization or asexual reproduction is possible. In the gonochore *E. lisbethae*, mothers and offspring were also electrophoretically identical, but variation in DNA fingerprints was consistent with cross-fertilization. Similar DNA fingerprint differences between mother and offspring indicate cross-fertilization also occurs in the gonochore *E. ritteri*. No mother-offspring comparisons were performed on *E. fernaldi*, as this species was not observed brooding during this study.

Allozymes and DNA fingerprints were also used to compare population genetic structure in the four brooding *Epiactis* species to that in the broadcasting species *Anthopleura elegantissima*. Results were generally consistent with expectations based on larval dispersal potential, but were only weakly correlated with expectations based on mating system. The brooding *Epiactis* species generally had less variation within- and more variation between-sites than the broadcasting species. However, outcrossing *Epiactis* species did not always have greater within-population variation or less population subdivision than asexual or self-fertile species.

Both allozyme and DNA fingerprint data clearly distinguish *E. prolifera*, *E. fernaldi*, and *E. ritteri* from each other. However, the taxonomic status of *E. lisbethae* is unresolved. *E. prolifera* and *E. lisbethae* were electrophoretically indistinguishable, but DNA fingerprinting showed some differentiation between sympatric populations. Phylogenetic reconstructions based on allozymes and on preliminary DNA fingerprint and DNA sequence data (ITS1) are consistent with polyphyly in the genus *Epiactis*, with the two internal brooders (*E. fernaldi* and *E. ritteri*) and the two external brooders (*E. prolifera* and *E. lisbethae*) arising independently.

# Rotifer Population Distribution in the Oxycline of "la Laguna de la Cruz": Metabolic Adaptations of *Brachionus plicatilis* to Microaerobic Conditions

**Esparcia, C. A.**
**University of Valencia (Spain), 288 pp.**

This work is divided in two parts. In the first part the vertical distribution of planktonic rotifers is described in relation to some physicochemical parameters in a small meromictic lake. Rotifers concentrate their populations at the depths with intense gradients. Two rotifers groups can be differentiated: 1) hypolimnetic and oxyclinal species such as *Anuraeopsis miraclei*, *Filinia hofmanni*, *Anuraeopsis fissa*, *Polyarthra dolichoptera* and *Keratella quadrata*; and 2) epi-metalimnetic species such as *Hexarthra mira*, *Trichocerca similis*, *Synchaeta pectinata*, *Asplachna girodi*, *Ascomorpha saltans* and *Ascomorpha ecaudis*. The new, recently described, species *A. miraclei* is the most highly associated to extreme microaerobic conditions.

The second part is devoted to an experimental study of the rotifer *B. plicatilis* for determining the relationships between oxygen limitation and the metabolic adaptations of rotifers to it. Previously some methodological problems were solved which proved to be useful for controlling oxygen conditions in other rotifers groups and for maintaining long-term *B. plicatilis* populations with the newly assayed food source, the alga *Tetraselmis* sp. thermally treated (65-70 B0C for 90 min.). The population dynamics of *Brachionus plicatilis* was studied under controlled oxygen conditions. This rotifer is able to maintain relatively high-density populations in oxygen concentrations below 1 mg/l, for more than one month, although its growth and metabolism is extremely reduced. Major features of population growth related to oxygen concentration are discussed. Activities of 10 enzymes and accumulation of two metabolites under experimental hypoxia were also investigated in the rotifer *Brachionus plicatilis*. Pyruvate kinase, lactate dehydrogenase, malic enzyme, phosphoenolpyruvate carboxykinase, malate dehydrogenase and fumarase activities showed great increase at low oxygen levels. Alcohol dehydrogenase activity was not detected. Alanine concentration showed a increase with low oxygen levels, which is interpreted as enhanced proteolysis. These results show that *B. plicatilis* use the lactate pathway for anoxic glucose metabolism, and suggest that the glucose-succinate pathway would also function at low oxygen concentrations. This pattern is consistent with the phylogenetic position of rotifers.

## Fluxes and Metabolic Pools of Amino Acids in Algal-Cnidarian Symbioses

**Ferrier, M.D. 1992**
**University of Maryland at College Park, 177 pp.**

The uptake and release of dissolved free amino acids (DFAA) by four coral species and the sea anemone *Aiptasia pallida* was investigated using high pressure liquid chromatography and radioisotopic methods. All species exhibited net uptake of a mixture of eight amino acids at near-ambient (low nanomolar) levels. Further studies using *A. pallida* indicated that DFAA uptake is animal mediated, energy requiring, and likely coupled with influx of $Na^+$. Under conditions of food deprivation, endosymbiotic dinoflagellates (zooxanthellae) indirectly enhanced DFAA uptake by providing the animal with a ready source of energy in the form of translocated photosynthetic products. Amino acid uptake may be particularly important for nonfeeding, early life-history stages and cnidarian species inhabiting DFAA-enriched environments.

*A. pallida* released minimal amounts of DFAA. However, the loss of combined amino acids from the symbiosis can be substantial.

Changes in the size and composition of the internal free amino acid (FAA) pools of cultured and freshly isolated zooxanthellae were used to assess algal nitrogen status. Since N-rich cultured algae sequestered basic amino acids (particularly Arg) for nitrogen storage, FAA ratios of Arg:Glu, Arg:Total, and Basic:Total were responsive indicators of N-sufficiency. Ratios were elevated in algae freshly isolated from *A. pallida* which were fed daily but declined in algae from hosts fed less frequently. Thus, in oligotrophic environments the N-status of zooxanthellae largely reflects the feeding history of their host.

Changes in host FAA pools were also monitored as a function of feeding history and inorganic nitrogen availability in both zooxanthellate and aposymbiotic anemones. Zooxanthellate animals fed daily exhibited much greater protein biomass and biomass-normalized FAA pool size than all other treatments. However, Tau:Gly ratios indicated that, under conditions of food deprivation, zooxanthellate anemones displayed greater nutritional stress than their aposymbiotic counterparts. Making inorganic N available during food deprivation decreases this stress in zooxanthellate anemones. These findings suggest that, with regard to nitrogen metabolism, the nature of the symbiotic relationship may be influenced by the availability of nitrogen.

# Impact of Hydrodynamic Factors on Photosynthesis and the Fate of Primary Production in an Oligotrophic Lake

**Frenette, J.J. 1993**
**University of Laval (Canada), 177 pp.**

I compared the production ecology of phytoplankton from two basins of an oligotrophic lake which are characterized by the presence and absence of summer stratification. The objective of this study was to assess the impact of mixing and stratification of the water column on phytoplankton photosynthesis and the fate of primary production.

My results firstly show that estimates of photosynthetic capacity ($P_{max}$) and efficiency (a), calculated using photosynthesis vs irradiance curves, vary depending on the model used. Estimates of $P_{max}$ using the exponential and hyperbolic tangent models are in good agreement (4% difference). The same comparaison for a shows poor agreement (24% difference between the two models). The lack of agreement increases when an intercept parameter is included in the models.

The relationship between the size-distribution of phytoplankton biomass and production was used to characterize the fate of primary production on daily and seasonal time scales. The phytoplankton community was dominated by small cells (pico- and nanoplankton), which reflects the oligotrophic status of the lake where competition for nutrients was likely to favour smaller-sized phytoplankton. The nanoplankton fraction accounted for most of the seasonal change in total biomass and production, whereas the contribution of picoplankton to both biomass and production remained relatively constant throughout the season. The observed seasonal variations in the size structure of phytoplankton do not agree with the usual paradigm of dominance of small organisms during the summer stratified period, and of larger algae during the mixing events of the spring and autumn. The relative constancy of picoplankton biomass throughout the season as well as the close relationship between potential growth and loss rates suggest an equilibrium controlled by herbivore grazing. In such environments where allochthonous nutrient inputs are limited, the principal source of nutrients would be autochthonous (recycling within the mixed layer) and mixing and stratification processes would not have a major impact on productivity.

The size-fractionated photosynthesis was used to characterize the influence of environmental factors on the phytoplankton community, on daily and seasonal time scales. Seasonal variations of $P_{max}$ showed size- related differences, with maximum values in July for the picoplankton and in November for the nanoplankton. Results also indicate that picoplankton require less light to saturate photosynthesis, and can sustain a wide variation in ambient irradiance, which suggests a euryphotic capacity of adaptation.

Diel periodicities of $P_{max}$ and a were observed for both the pico- and the nanoplankton, each size fraction exhibiting distinct patterns of variability in the timing and amplitude of daily oscillations. Maximum photosynthetic capacity was generally observed for the two size fractions around noon and in the morning, but without synchronicity. The picoplankton exhibit larger amplitudes in the oscillations of $P_{max}$ and a than the nanoplankton, which suggests differences in the photonutritive history of each size fraction. Hydrodynamic differences in the two basins account for the adaptation to high irradiances of picoplankton in Basin 1. The vertical and seasonal changes in photosynthetic parameters show that both fractions are photoadapted to their environment and that the stratification and mixing regime modifies the photosynthetic response depending on the physiological characteristics associated with size.

# Water Quality Dynamics in Aquaculture Ponds: An Investigation of Photosynthetic Production and Efficiency Variations

**Giovannini, P. 1994**
**University of California at Davis, 192 pp.**

This work, divided into four sections, describes several interrelated areas of research dealing with the analysis and monitoring of pond primary production. The first section discusses the development and testing of a field respirometer system designed to measure water column respiration rates in quickly darkened samples at frequent intervals over a diel period. Water column respiration is a major sink for dissolved oxygen, and it is vital that respiration rates be determined before accurate estimates of gross primary production can be made. Because of the importance of the dynamics of gross production in determining the functioning of the primary production system, this system enables analysis of pond dynamics not previously possible. The tri-hourly respiration and net production rate data gathered with the respirometer system are used to calculate short term changes in the apparent gross primary production rates over the diel period. The results of experiments with the respirometer system show that water column respiration rates follow distinct diel patterns which are not simply correlated with light, temperature or primary production. Data collected from a series of indoor tank experiments and field tests at the Asian Institute of Technology are used for further analysis in the following sections.

The second section uses data collected with the respirometer system to examine changes in the efficiency of primary production over diurnal periods. Using the calculated apparent gross production rates, the efficiency of gross primary production with respect to solar radiation is calculated before and after fertilization. In addition, efficiency of net production with respect to light is calculated, as well as the ratio of gross production rates to measured respiration rates. Results show that efficiencies increase with fertilization, and that this analysis can provide a basis for management of nutrient inputs.

The third section presents a model for the calculation of the light saturation intensity for phytoplankton populations, and uses data provided by the respirometer system to test the model. The light saturation intensity is a common parameter used in photosynthesis production models to quantify the light sensitivity of phytoplankton. Although this parameter is know to change over time, it is commonly specified as a constant in production models. The purpose of this section is to calculate the light sensitivity of the phytoplankton cultures from an analysis of observed gross production rates with respect to light. The results of this section show that commonly used photosynthetic production equations may overestimate production by assuming instantaneous light response by algal cultures, and that changes in phytoplankton light sensitivity may occur when photoinhibition is present.

The final chapter presents the derivation of theoretical models for the optimization of photosynthetic production in a pond based on three physical parameters - light, depth and turbidity; and three biological parameters - respiration per unit chlorophyll-*a*, maximum production per unit chlorophyll-*a*, and phytoplankton light saturation intensity. An expression is derived for the optimum solar light intensity for a pond water column, based on the physical parameters of the pond and the light saturation intensity of phytoplankton . This expression can be used to compare solar radiation at the pond site with the optimum light levels calculated for given depth and turbidities. Conversely, expressions for optimization of net photosynthetic production are derived by calculating the optimum depth or algal turbidity for a given solar light intensity. These models may be used as a basis for design and operation of pond systems.

# The Physical Oceanography and Ecology of Upwelling Shadows

**Graham, W.M. 1994**
**University of California at Santa Cruz, 205 pp.**

Interactions between larval behavior and local hydrography affect settlement patterns of the crab, *Cancer gracilis*, in northern Monterey Bay. An upwelling shadow is a typical feature of northern Monterey Bay during upwelling season (~March to August) and is a dynamic response to upwelling north of the bay as cold, upwelled water is advected into the bay, re-circulated, entrained and subsequently heated. This upwelling shadow is thin (<15 m thick) vertically trapped, warm patch of water that behaves much like an estuarine plume. A quasi-persistent (weeks to months) front with both shear and buoyancy components separates the upwelling shadow from recently upwelled water offshore.

Within this front, dense aggregations of the scyphomedusa *Chrysaora fuscescens* occur. Uniformly oriented horizontal swimming of these medusae further minimizes the swarm's dispersal. Megalopas of the brachyuran crab *Cancer gracilis* tend to cling to drifting and slow-moving materials, and they are accumulated on the jellyfish where they may remain for several months as juveniles. While on medusae, crabs probably experience protection, enhanced growth, increased dispersal and decreased loss due to offshore advection.

The jellyfish-front interaction causes most juvenile crabs to settle on the sea floor ~4-8 km from shore during upwelling seasons (March-August). In the absence of jellyfish swarms, as during the 1992 El Nino Southern Oscillation, *Cancer gracilis* settles much closer to shore. This study provides evidence that specific larval behavior is an integral component of the physical-biological interactions which determines juvenile settlement patterns.

# Wave-Forced Porewater Mixing and Nutrient Flux in a Coral Reef Framework

**Haberstroh, P.R. 1994**
**University of Hawaii at Manoa, 249 pp.**

Convective water flow, rather than molecular diffusion, is thought to dominate the exchange of dissolved material between interstitial water of coral reefs and the overlying water. Surface waves passing over coral reef flats should induce an oscillatory motion of framework interstitial waters and, in the presence of a downward increase in porewater nutrient concentrations, may enhance through dispersion the flux of interstitial nutrients to the overlying waters and marine organisms at the reef surface. These processes were examined through the use of a cross-reef array of well point-samplers, pressure transducers and electronic recording of hydraulic head variations on and within the framework of a small patch reef, Checker Reef, located in central Kaneohe Bay, Oahu, Hawaii.

Interstitial porewaters at all reef sites were characterized by a $NO_3$+$NO_2$ concentration maximum at sediment depths of 5 to 10 cm, and progressively-increasing concentrations of $PO_4$, $NH_4$ and Si with sediment depth. Spectral analyses of the time series of the mean-normalized pressure head allowed the development of two hydrological models of wave-induced chemical flux, macroscopic dispersion and megadispersion, and allowed the comparison to fluxes driven by molecular diffusion. Nutrient fluxes were also measured directly using stirred benthic chambers. Wave-induced pressure head was usually measured at 1- and 2-m framework depth, although it was measured in detail over the upper meter of the fore-reef framework. Spectral analysis of the time series of pressure head variations yielded relationships between wave-frequency and (1) the spectral variance of the mean normalized amplitude, and (2) the cross-spectral phase and coherence between the mean-normalized amplitude and the net head. At sediment depths of 2 m, waves with periods >2-20 s were not detected, although internal waves with periods of around 30-60 s were still present. Nutrient fluxes driven by molecular diffusion were usually $\geq$1 μmoles $m^{-2}$ $d^{-1}$, while those due to macroscopic dispersion for February, 1992, were 1-10 μmoles $PO_4$ $m^{-2}$ $d^{-1}$, 1-73 μmoles $NO_3$+$NO_2$ $m^{-2}$ $d^{-1}$, 6-41 μmoles $NH_4$ $m^{-2}$ $d^{-1}$, and 10-198 μmoles Si $m^{-2}$ $d^{-1}$. The mean fluxes for February 1992 by wave-driven megadispersion, however, were 140-1540 μmoles $PO_4$ $m^{-2}$ $d^{-1}$, 60-27220 μmoles $NO_3$+$NO_2$ $m^{-2}$ $d^{-1}$, 640-15560 μmoles $NH_4$ $m^{-2}$ $d^{-1}$, and 1780-70170 μmoles Si $m^{-2}$ $d^{-1}$.

The close agreement between the calculated megadispersive fluxes and flux estimates by previous researchers based on hydrological measurements, and on $^{222}Rn$ and salinity variations, suggests that wave-induced flux by megadispersion was the controlling mechanism driving nutrient fluxes through the framework pore space. Megadispersion-driven N-uptake rates occurring below 10-25 cm framework depth (20-2900 μmoles N $m^{-2}$ $d^{-1}$) also agreed closely to denitrification rate measurements of other researchers (60-9800 μmoles N $m^{-2}$ $d^{-1}$). The large difference between the modelled megadispersive flux and observed benthic chamber-derived fluxes indicated substantial (90%) autotrophic consumption of interstitial nutrients within the upper few centimeters of the framework, and at rates similar to that of the overlying reef autotrophs. The inferred high nutrient turnover occurring within the upper 5-10 cm of the framework may be due to autotrophic growth promoted by the selective transmission of light through opaque carbonate sediments. Nutrient fluxes within coral reef systems appear to be sustained by physical, rather than biological, forcing mechanisms.

# USEPA Water Quality Criteria for Copper: I. Exceedence of Criteria in Freshwater Streams. II. Influence of Dissolved Organic Matter on Toxicity

**Hamblin-Katnik, C. 1993**
**George Mason University, 203 pp.**

This paper seeks to evaluate the USEPA Water Quality Criteria for copper, where copper is measured by the total recoverable method and the criteria are based on water hardness. Photo-oxidized stream water (pH 7.69 +/- 0.22, water hardness 81 mg/L) was used to determine the $LC_{50}$ (43.2 µg/l) of copper for *Daphnia pulex*. Graded dilutions of nonphoto-oxidized stream water were used in a toxicity test with constant hardness (81 mg/l $CaCO_3$) to determine the effects of organics on *Daphnia* mortality. It was found that mortality was inversely related to dissolved organic matter; mortality was directly related to cupric ion content; and cupric ion content was inversely related to organic matter. These data suggest that dissolved organic matter (in addition to hardness) has a significant impact on copper toxicity. A probabilistic deterministic methodology was used to determine if the EPA Criterion Maximum Concentration (CMC) for copper was being violated in streams at five sites that received urban runoff. Each site exhibited some degree of CMC exceedence. A water quality criterion for copper based solely on hardness can lead to gross misrepresentations of the toxicity in the water body. This uncertainty could result in regulatory as well as private sector inefficiencies should the criteria be used in any type of standard setting, and leads the scientific community to ignore further interactions among water quality parameters that may mitigate or strengthen the toxic effects of copper to aquatic organisms. Criteria concerning individual speciation of copper have not been promulgated and individual species impacts are not distinguishable given the total recoverable metal measurement method.

# Biological and Physical Processes Involved in the Larval Survival and Recruitment of Bluefish, *Pomatomus Saltatrix* (Pisces: Pomatomidae), along the Eastern Coast of the United States

**Hare, J.A. 1994**
**State University of New York at Stony Brook, 264 pp.**

The purpose of this dissertation is to examine the role of biological and physical processes in the larval survival and estuarine recruitment of bluefish, *Pomatomus saltatrix*, along the eastern coast of the United States. As an initial analysis, information regarding bluefish larval distribution is reviewed and it is hypothesized that the bluefish population spawns continuously as opposed to in distinct events as previously believed. If bluefish do spawn continuously, there must be a mechanism that creates the consistent appearance of two estuarine juvenile cohorts, a pattern observed in the Middle Atlantic Bight since the 1920's. A simple larval transport model is developed and this model indicates that transport processes can explain the appearance of two juvenile cohorts from a continuous production of offspring.

Following this model, the transport of South Atlantic Bight-spawned bluefish to Middle Atlantic Bight estuaries is examined in more detail. A variety of biological and physical data are analyzed and a mechanistic transport route is proposed. Spawning occurs on the outer South Atlantic Bight shelf in Outer Carolina Shelf and Gulf Stream water. Following northeastward transport in association with the Gulf Stream, cross-slope transport occurs via warm-core ring streamers. Bluefish young then accumulate at the surface shelf-slope temperature front at the Middle Atlantic Bight shelf break. When this front breaks down due to increased solar radiation in the late spring, young bluefish apparently swim across the shelf to their nearshore juvenile habitats. The specific mechanisms of this proposed route need to be further evaluated, but the indication is that variation in certain aspects of this transport may cause variation in the estuarine recruitment patterns of South Atlantic Bight-spawned bluefish.

Regarding biological processes, the growth-mortality hypothesis (i.e. the faster an individual grows, the higher it's probability of survival) is evaluated for a cohort of bluefish larvae. Initially the otolith record of size and ontogeny is examined and it is concluded that at a given age, an individual with a larger otolith also has a larger body size. Otolith radii at various ages are then compared among individuals and this comparison indicates that larvae with larger otoliths at age had a higher probability of survival. Coupling this finding with the initial otolith work indicates that individuals which grow faster have a higher probability of surviving the larval stage, thereby providing support for the growth-mortality hypothesis.

In conclusion, both biological and physical processes act in concert to shape bluefish larval survival and subsequent recruitment. This work provides a foundation for further examination into larval survival and recruitment processes of bluefish, as well as the many other species whose offspring utilize the continental shelf of the eastern coast of the United States.

# Competition in a Seasonal Environment: *Daphnia* Population Dynamics and Coexistence

**Hu, S.S. 1994**
**Michigan State University, 109 pp.**

Similar species of zooplankton commonly replace one another in a seasonally predictable fashion. Often, this species succession is explained by invoking predation (e.g. trade-off between predator vulnerability and competitive ability). The importance of resource partitioning or seasonal changes in competitive ability is rarely explored. In Gull lake, a large mesotrophic lake characterized by a low level of zooplanktivory, I documented a consistent (multi-year) seasonal replacement of one *Daphnia* species (*D. pulicaria*) by another (*D. galeata mendotae*) in the summer epilimnion. In this thesis I address the hypothesis that these *Daphnia* species coexist by a seasonal shift in competitive capability (temporal partitioning).

A weekly sampling of zooplankton, phytoplankton and other limnological measurements was carried out in summer of 1989,1990 and 1991. A correlation analysis suggested that neither predation nor abiotic factors fully explained the *Daphnia* seasonal replacement. Using a seasonal series of in situ predator exclosures, I manipulated densities of the two *Daphnia* species and measured their performance and intensity of inter- and intra-specific competition. I also performed a series of life table experiments and *in situ* culture experiments to assess the influence of natural food and temperature conditions on population growth of the two species.

*Daphnia pulicaria* appears to have a competitive advantage in conditions of high quality food and low temperature (i.e. spring and early summer). In contrast, *D. galeata mendotae* is competitively superior in conditions of low quality food and warm temperature typical of late summer. Hence, seasonal variation in resources and temperature can explain the seasonal succession and long-term coexistence of these species. I also investigated diel vertical migration of the *Daphnia* in Gull Lake to assess the theory that nighttime migration represents a way to avoid visual predators during day, yet exploit a richer resource availability in surface waters. Results suggested that the major benefit of nighttime movement into surface waters was an acceleration of embryo development due to warmer temperatures, but not a feeding gain.

# Regeneration and Recycling of Biologically Required Trace Metals by Marine Plankton Communities

**Hutchins, D.A. 1994**
**University of California at Santa Cruz, 91 pp.**

A series of experiments was carried out to determine whether regeneration and recycling of cellular Fe, Zn and Mn by marine plankton communities could be an important source of biologically required trace metals to support phytoplankton growth. Although regeneration has long been known to be a major source of N and P to phytoplankton, nothing was previously known about the potential of trace metals to support regenerated production, despite recent evidence for Fe as a limiting nutrient in some oceanic regimes.

Studies in which Fe-labeled phytoplankton cultures were added to natural plankton communities demonstrated rapid transfer of Fe from the added inoculum to indigenous cells, on a time scale of days. Size-fractionation and microautoradiography were used to quantify and compare Fe recycling in plankton communities from the equatorial Pacific and Monterey Bay, California.

Laboratory studies in which phytoplankton and protozoan cultures labeled with $^{59}Fe$, $^{65}Zn$ and $^{54}Mn$ were used as prey for crustacean and protozoan grazers demonstrated that, as is the case for major nutrients, grazers play an important role in remineralizing cellular trace metals.

A comparison of Fe, Zn , Mn and N transfer from added cyanobacteria to large cells in Monterey Bay revealed differences in recycling efficiencies for the three trace metals. The order of transfer efficiency was Fe>Zn>Mn; of the three metals, Fe most closely approached the transfer efficiency measured for N.

These data demonstrate that trace metals can be quickly and efficiently recycled and reused by plankton communities, and in fact in areas of low trace metal inputs regeneration may be the major source supporting phytoplankton growth. Driven by the ubiquitous activities of zooplankton grazers, Fe in particular is conserved by the biological community nearly as efficiently as the classical recycled element N. This research suggests that this biological recycling loop could be an important element of the marine biogeochemistry of trace metals, and emphasizes the role of trace metals as required nutrients, with the full range of complex biological and chemical interactions that such a classification implies.

# Cyanobacterial Waterblooms: The Role of Buoyancy in Water Columns of Varying Stability

**Ibelings, B.W. 1992**
**University of Amsterdam (Netherlands), 171 pp.**

Nuisance blooms of cyanobacteria are a clear expression of the eutrophic state of lakes, rivers, and coastal waters in which they occur. There are three prerequisites for formation of surface-water blooms: i) a high biomass, ii) buoyancy of the cells, iii) a stable water column. I studied these conditions and the formation of blooms in relatively shallow lakes in the Netherlands. Gas vesicles provided buoyancy to the cyanobacteria. Supported by high nutrient concentrations in the lakes the cyanobacteria established a high biomass, benefiting from their buoyancy under conditions of partial water-column stability. During these periods mixing was restricted to a shallow near-surface layer. The colonial cyanobacteria floated up into this layer, thus increasing their daily light dose, and outcompeting non-buoyant competitors in the phytoplankton. Periods with intensive mixing arrested growth of colonial cyanobacteria, presumably because the cyanobacteria are not well adapted to the fast changing light conditions that result from mixing (see second paragraph). The likelihood of persistent bloom formation, however, was higher after a short period of deep mixing, following a period of stable conditions. Deep mixing imposed a low average irradiance on the phytoplankton; conditions that stimulated gas vesicle synthesis. The now over-buoyant colonies possessed 50% more gas vesicles than needed for neutral buoyancy. They could no longer lower their buoyancy sufficiently to sink, and remained at the lake surface (the main mechanism for the regulation of buoyancy in these lakes was through the accumulation of dense photosynthate, mainly glycogen). However, colonies that are acclimated to low average irradiance *prior* to bloom formation can easily get photodamaged during exposure to high irradiance at the lake surface. This was found in the top layer of blooms by measuring rates of photosynthesis using oxygen microelectrodes, that allowed analysis with sufficient high spatial resolution.

Acclimation to high irradiance, as well as to fluctuating light was studied in more detail in cultures of cyanobacteria and green algae receiving computer controlled variable light regimes. These regimes simulated the natural light environments resulting from different degrees of wind induced mixing. Acclimation of the photosynthetic apparatus to fluctuating light was more reluctant in the cyanobacterium. Partially because of a conservative carotenoid composition, that showed no acclimation to the diel variation in irradiance. The sustained presence of the photoprotective xanthophyll zeaxanthin led to a detrimental loss of excitation energy at low irradiance (as judged from patterns of fluorescence quenching). In contrast, eukaryotic green algae have a xanthophyll cycle, in which zeaxanthin is only present during over-excitation of photosystem II. The study of acclimation to high irradiance, in a light regime simulating surface bloom formation, showed that the cyanobacterium was also less flexible in this respect. These results underlined the need for cyanobacteria to have a fine tuned buoyancy regulation. This reduces fluctuations in irradiance by allowing the colonies to float into the illuminated near surface mixed layer, but at the same time avoids over-exposure.

# Landscape Ecology and the Functions of Marine Soft-Sediment Habitats: How Seagrass Landscapes Influence Growth and Survival of a Marine Invertebrate

**Irlandi, E.A. 1993**
**University of North Carolina at Chapel Hill, 138 pp.**

Seagrass beds occur in a variety of spatial configurations at both high-energy shoals and low-energy quiescent bays. I applied a landscape-ecology approach to examine how habitat patch size under high- and low-energy conditions influenced growth and survival of large (41.9 mm) and small (22.3 mm) hard clams, *Mercenaria mercenaria*, and how the spatial configuration (i.e., percent coverage) of seagrass patches influenced survival and siphon cropping of small clams.

Large and small clams grew faster within vegetation than out at both high- and low-energy sites. Within the vegetation, growth of large clams was faster in medium sized patches of seagrass (2-3 m across) than in small patches (1 m across) and was intermediate in large patches (>4-5 m across). Growth of small clams was independent of the two seagrass patch sizes tested (large vs. small). Although small clams grew significantly more within seagrass under both high- and low-energy conditions, the effect was significantly more pronounced at high-energy sites than at low. The effect of seagrass cover on clam growth appears to be the result of a complex interaction among food supply, predation disturbance, and sediment stability with the relative importance of these processes varying with size of the clam, hydrographic regime, habitat patch size, and local site differences.

Survivorship of large clams was independent of presence of seagrass and seagrass patch size, but approximately three times as many clams were recovered live from low-energy than from high-energy sites. An opposite pattern occurred for small clams with significantly fewer clams being recovered live from two low-energy sites than from one high-energy site. Small clam survivorship also increased with the areal extent of seagrass cover. Twice as many clams were recovered live from large patches of seagrass than from small, and 18 times more were recovered from large patches than from unvegetated sediments. Survivorship patterns of small clams were positively correlated to changes in below-ground biomass and shoot densities among sites and seagrass treatments as well as to patterns in growth of clams.

When clams were placed in both the vegetated and unvegetated portions of a 100-$m^2$ area of seafloor nearly twice as many clams were recovered live with 99% seagrass cover than with 23% seagrass cover, while survivorship was intermediate with 70% cover. Mean adjusted siphon weights were also approximately 76% heavier from the 99% seagrass cover treatment than from the 70% or 23% cover treatments. Survivorship of clams placed within an equal area of seagrass (100-$m^2$) in very patchy, patchy, and continuous spatial configurations was 40% higher in the continuous seagrass treatment than in either of the two patchy treatments.

I applied a landscape-ecology approach to an aquatic environment and demonstrated that trophic transfer of energy in seagrass ecosystems changes with patch size and spatial configuration of the habitat. These results have direct application to restoration and management of seagrass beds.

# Direct and Indirect Effects on Planktonic Ciliate Assemblages

**Jack, J.D. 1993**
**Dartmouth College, 185 pp.**

A series of experiments examined the direct and indirect effects of metazooplankton and suspended clays on planktonic ciliate assemblages. The presence of suspended fine (particle size <1 mm) and coarse (particle size < 2 μm) clay suppressed the reproductive rate of the ciliate *Strobilidium gyrans* by up to 69 % but had no effect on three other common ciliates.

In laboratory experiments with excess food, four of six ciliates were just as susceptible to the small cladoceran *Bosmina longirostris* as to the much larger *Daphnia pulex*. The jumping response of the ciliate *S. gyrans* appeared to be an effective defense against *B. longirostris*. Thus, cladocerans can have significant, negative, direct effects on ciliate species.

Natural microzooplankton communities were significantly suppressed by *Daphnia* in laboratory experiments. Most rotifer species were suppressed by *D. pulex* but not by the smaller daphniids. Small ciliates (< 30 μm), were adversely affected by all of the cladoceran treatments, while several larger ciliates (> 81 μm) were unaffected in all such treatments. In most cases, the suppression of ciliates and rotifers was attributable to direct effects of the cladocerans.

Bottle experiments were performed at intervals from early June to late November in two lakes to assess the effect of temporal changes in metazooplankton community structure on ciliate assemblages. Throughout the study period rotifers had strong positive indirect effects on larger (> 40 μm) ciliates with escape responses and slight negative indirect effects on small ciliates when crustacean zooplankton were also present. The copepods had strong negative direct effects on all but the largest ciliates. Large cladocerans had substantial direct effects on ciliates, while smaller cladocerans sometimes had measurable indirect effects. These experiments show that the importance of top-down effects on ciliates varies with the changing structure of metazooplankton community.

# Spatial and Temporal Patterns of Nitrogen Fixation and Denitrification in the Intertidal and Subtidal Sediments of a Mediterranean-Type Estuary: Tomales Bay, California

**Joye, S.B. 1993**
**University of North Carolina at Chapel Hill, 227 pp.**

Microbially-mediated nitrogen transformations were examined at two intertidal and three subtidal locations in Tomales Bay, California. Intertidal sediments were inhabited by productive microbial mat communities and served as net sources of combined nitrogen since nitrogen fixation rates exceeded denitrification rates. Though potential denitrification rates were positively correlated with nitrogen fixation rates over diel cycles, the two processes were comparable in magnitude only at night throughout most of the year.

Both nitrogen fixation and denitrification were inhibited by photosynthetic oxygen production, but denitrification was more strongly inhibited than nitrogen fixation. This inhibition of denitrification served to limit losses of combined nitrogen from microbial mat communities and resulted in a net input of combined nitrogen to intertidal environments during most of the year.

However, during winter, a different pattern was observed with denitrification rates exceeding nitrogen fixation rates. At this time, low rates of photosynthesis reduced oxygen inhibition of denitrification and high water column concentrations of dissolved inorganic nitrogen depressed nitrogen fixation. Both of these factors led to a domination of the net nitrogen budget by denitrification during winter.

In subtidal sediments, denitrification rates exceeded nitrogen fixation rates and these regions served as net sinks for combined nitrogen. Nitrogen fixation was present throughout the upper 50 cm of sediment and showed no apparent seasonal pattern. Rates of nitrogen fixation amouted to at most 30% and on average 10% of denitrification rates. Denitrification rates were highest in the upper 3 cm of sediment and activity extended to significant depth (40 cm) in these sediments throughout the year. High rates of denitrification were fueled by nitrate derived from both in situ nitrification and by the diffusive flux from the overlying water column to the sediment. Seasonally, maximum denitrification rates were observed during summer and fall with lower rates observed during winter. Denitrification showed a strong positive correlation with bottom water temperature and nitrification.

Both denitrification and nitrification were higher in vegetated compared to unvegetated subtidal sediments in the inner portions of the Bay. However, no significant spatial trend in denitrification was observed along a horizontal transect running from the headwaters to the mouth of the Bay. An interesting dichotomy exists between the intertidal and subtidal sediments of Tomales Bay. Intertidal sediments were net autotrophic, with production exceeding respiration. These regions served as net sources of combined nitrogen, due primarily to the activity of autotrophic, nitrogen-fixing cyanobacteria. In contrast, heterotrophic subtidal sediments served as net sinks for combined nitrogen. Because the area of subtidal sediments exceeds that of intertidal sediments (28 versus 3 $km^2$), the Bay as a whole functions as a sink for combined nitrogen with denitrification exceeding nitrogen fixation rates by 5 to 15 times.

# Toxic Secondary Metabolites from *Microcystis* Flos-Aqae Strain PCC7806: Biochemical Characterization by Natural and Laboratory Investigations

**Jungmann, D. 1994**
**University of Kiel (Germany), 101 pp.**

The chemical interactions between *Microcystis* and *Daphnia* were investigated. My goal was to characterize the compound from *Microcystis*, which was responsible for its toxicity to *Daphnia*. The combination of a so-called signal compound, which affects the filtering rate of daphnids and a toxic compound were suspected to promote *Microcystis* mass development under ideal environmental conditions. The *Microcystis* strain PCC7806 was chosen to establish a standard procedure to extract the compound that is toxic to *Daphnia pulicaria*. A *Daphnia*-biotest was established and quantification of toxicity was possible by calculating the LC50 of a water extract from *Microcytis*.

The *Daphnia*-biotest was used to investigate the acute toxicity of microcystin-LR and 3-desmethyl-microcystin-LR. These cyclic hepatotoxic heptapeptides, which originated from the secondary metabolism of *Microcystis*, were suspected as a possible source of toxicity to daphnids. The toxicity to daphnids was found in the microcystin-free fraction, hence, I concluded that *Microcystis* contains other compounds which are more toxic to *D. pulicaria*. Therefore, I discriminated between hepatotoxic microcystins and the compound that is toxic to *Daphnia*, termed DTC (*Daphnia*-toxic compound).

Investigations of toxicity of partially purified water extracts from natural *Microcystis* samples, collected in the Bautzen Reservoir near Dresden, showed a higher toxicity to *D. pulicaria* during summer than extracts from laboratory strains. Moreover, a comparison of microcystin content and *Daphnia*- toxicity of the sampled material showed no correlation. This leads to the conclusion that DTC synthesis is also independent of microcystins.

The partially purified water extract from *Microcystis* PCC7806 was reduced in volume and biochemically investigated. The DTC was temperature stable within a range of -18 $^{o}$C to 121 $^{o}$C; it was resistant to degradation by two isolated bacteria and two unspecific proteases; DTC was stable and water soluble between pH 2 and pH 12; charge of the DTC was used for purifying with a strong anion-exchange-resin using FPLC equipment; the molecular weight was determined to be between 1.0 and 3.2 kDA by gel filtration using FPLC equipment. UV/VIS spectra of the final fractions were made.

# Biogeochemical Cycling of Iron in Anoxic Environments: The Importance of Fe Speciation and Bacterial Fe Reduction

**Kostka, J.E. 1992**
**University of Delaware, 243 pp.**

Reactive Fe has a profound influence on the cycling of nutrients in coastal marine and aquatic environments. Though most studies have concentrated on Fe cycling in porewaters, most reactive Fe is present in the solid phase of sediments. Further, much of the release or solubilization of solid phase reactive Fe is thought to be mediated by organisms. This study was initiated to develop and implement methods to study the biogeochemical cycling of Fe in coastal marine environments and to assess the role of metal-reducing bacteria in the coupling of Fe and C cycles.

A calibrated chemical extraction scheme was developed for partitioning reactive Fe minerals in marine sediments. Amorphous, highly reactive Fe(III) minerals were shown to comprise a large fraction (>45% of total Fe) and crystalline, less reactive minerals were also abundant (20-33% of total Fe) in the root zone of saltmarsh sediments. Iron sulfides, pyrite and acid-volatile sulfide (AVS), were measured to completely partition oxidized and reduced Fe fractions of the sediment. This extraction scheme was combined with an analysis of porewater chemistry to examine the seasonal cycling of Fe in sediments sampled from the root zone of Spartina alterniflora and in sediments overlain by a cyanobacterial mat. In 10 sediment cores taken over a 13 month period, a majority of solid Fe in vegetated sediments was observed to completely cycle between oxidized reactive Fe and reduced Fe as pyrite. In mat sediments, no seasonal trend was apparent and the speciation of reactive Fe revealed that a majority was reduced. Solid phase and porewater data supported the dominant role of Spartina roots and sediment bacteria in controlling the reactivity of Fe and its interaction with S cycling.

Sediment slurries, amended with microbial inhibitors, showed biological reduction of solid Fe(III) over formaldehyde-killed controls, exclusive of Fe reduction which may be attributed to biogenic sulfide. Microbial Fe(III) reduction was demonstrated in continental slope sediments and in summer saltmarsh sediments at in situ temperatures. The data suggested that sediment temperature and the presence of labile organic matter limit microbial Fe(III) reduction in these sediments.

The coupling of microbial growth to the respiration of Fe and S was studied in pure cultures of the Fe-reducing bacterium, Shewanella putrefaciens strain MR-4, isolated from the anoxic water column of the Black Sea. Growth data showed that a broad range of organic carbon compounds (C1 to C6) were oxidized during dissimilatory Fe(III) and thiosulfate reduction. Novel growth yields were similar with Fe(III) or S(IV) as electron acceptor and yields were comparable to those of other anaerobic respiratory bacteria. Because of their abundance in the marine environment, their carbon versatility, and their ability to transform large amounts of Fe or S, the S. putrefaciens group was suggested to play an important role in biogeochemical cycles.

# Regulation of the Maximum Quantum Yield of Phytoplankton Photosynthesis by Iron, Nitrogen, and Light in the Eastern Equatorial Pacific

**Lindley, S.T. 1994**
**Duke University, 136 pp.**

The surface waters of the eastern equatorial Pacific are characterized by persistent macronutrients and low phytoplankton biomass. The so-called "high nutrient-low chlorophyll" (HNLC) condition is enigmatic because the stable water column, high irradiance, and high nutrient concentrations would seem to be optimal for phytoplankton growth. Investigations spanning 25 years have shown that low iron concentrations may be partially responsible for the HNLC condition. The exact role of iron in the maintenance of HNLC is unknown; one hypothesis is that low iron availability limits the growth of rare large diatoms that could otherwise escape the control of small protistan grazers. Alternatively, iron may limit the photosynthesis and therefore growth of the existing equatorial flora.

Phytoplankton absorption coefficients and photosynthesis as a function of irradiance were measured on a transect across the equatorial Pacific at 140° W, on a survey in the vicinity of the Galapagos Islands, and during an open-ocean iron addition experiment performed 200 km south of the Galapagos. The maximum quantum yield of photosynthesis ($\phi_m$) was less than 50% of the expected nutrient-replete value in the upper 45 m at 0°, 140° W, in spite of $NO_3$ concentrations that exceeded 6 μM. The depression of $\phi_m$ indicated that photosynthesis was photoinhibited. The latitudinal pattern of $\phi_m$ corresponded closely to the concentration of $NO_3$ at 60m, a proxy for the rate of nutrient supply by upwelling. Quantum yield corrected for absorption by photoprotective carotenoids, however, was maximal at 12° N and declined linearly with latitude. This pattern corresponds with the eolian iron flux. The maximum quantum yield at 0°, 89° W was lower than at 0°, 140° W although the $NO_3$ concentration was higher. Photoinhibiton was apparent in the upper 30 m. Immediately downstream from the Galapagos, $\phi_m$ was enhanced by a factor of 2 relative to upstream values, and no photoinhibition was observed. Uncontained addition of $FeSO_4$ to the ocean's surface caused $\phi_m$ and the chlorophyll *a* concentration to double in the upper 35m. $\phi_m$ reached maximum values 1 day after iron addition. The rapid response to iron addition indicates that the increase in $\phi_m$ and chlorophyll *a* was due to the physiological response of the dominant phytoplankton rather than a rare subpopulation. These results demonstrate that iron availability regulates the photosynthesis and growth of the dominant equatorial flora. I hypothesize that iron stress increases the susceptibility of phytoplankton to photodamage, while abundant $NO_3$ allows repair of photodamage and thus maintains the equatorial productivity maximum.

# Effects of Benthic Macrofauna on Nitrogen Cycling and Oxygen Consumption of Estuarine Sediments

**Mayer, M.S. 1992**
**University of Maryland at College Park, 182 pp.**

Macrofauna can significantly increase benthic nitrogen cycling in estuarine systems. The nature and magnitude of macrofaunal effects on benthic nitrogen cycling vary among species and depend, in part, on animal behavior. Of the species examined, macrofauna that introduce oxygen to subsurface sediment significantly increased the activity of nitrifying bacteria. The nitrification potential of their tubes or burrows was 2- to 200-times greater than that of adjacent sediments and 1- to 61-times greater than that of surface (0-1 cm) sediments. The degree of enhancement of nitrification potential was influenced by sediment ammonium levels and organism irrigation behavior.

Animal-density manipulation experiments demonstrated that, *Loimia medusa*, a tube-irrigating polychaete, significantly increased benthic oxygen consumption and release of ammonium ($NH_4^+$) and nitrate ($NO_3^-$) from sediment when concentrations of $NO_3^-$ in the overlying water were low (3 μM). Increased $NO_3^-$ fluxes and mass balance and stoichiometric calculations indicate that *L. medusa* stimulated nitrification and denitrification. Worm respiration and excretion contributed substantially (> 50%) to its effect on sediment-water fluxes of oxygen and regenerated nitrogen ($NH_4^+$ plus $NO_3^-$ plus $N_2$ from coupled nitrification-denitrification). Indirect worm effects (stimulation of microbial activities and increased $NH_4^+$ export) accounted for 25% to 50%. Due to its stimulation of the transformation of $NH_4^+$ by nitrification and denitrification, more than half of the increased release of regenerated nitrogen exited as $NO_3^-$ or $N_2$.

A field study examining three benthic communities with different macrofaunal assemblages indicated that the nature and magnitude of macrofaunal effects on benthic nitrogen cycling varied with macrofaunal biomass and community composition, especially the relative abundance of irrigators and bioturbators. At one site, an abundant burrow-irrigating amphipod, *Leptocheirus plumulosus*, appeared to affect the porewater $NH_4^+$ profile and sediment-water fluxes of nitrogen by stimulating nitrification and denitrification. At a second site, a diverse community with bioturbators (23%) and irrigators (16% of total density and 53% of total biomass) caused thorough mixing of the top 9 cm of sediment and appeared to increase $NH_4^+$ release from sediment. At a third site with high biomass of *Mulinia lateralis*, the primary macrofaunal effect was substantial contribution of animal excretion to nitrogen release from sediments.

# Ecological Investigations of the Age-0 Fish Community in a Shallow Brackish Inlet of the Southern Baltic

**Mehner, T. 1992**
**Rostock University (Germany), 139 pp.**

Species composition, growth, and food consumption of age-0 fish were investigated in a brackish inlet of the Baltic. Fish larvae and juveniles were caught both in on- and offshore areas using a mini-bongo net and dip nets once a week between April and June in 1990 and 1991. Additionally, the succession of the zooplankton community was regularly observed.

Herring (*Clupea harengus*) and perch (*Perca fluviatilis*) were the dominant fish species. Their diet nearly exclusively consisted of nauplii, copepodite stages, and adults of the most abundant copepod species *Eurytemora affinis*. The uptake of larger prey, especially the mysid *Neomysis integer*, increased with length of fish. Growth rate of both species was estimated to be very high in comparison to values measured in other waters.

Distribution of fish was determined by salinity, water depth, and macrophyte cover of the bottom. Whereas the 0+ herring and gobies (*Pomatoschistus* sp.) were pelagic and preferred areas with about 4 - 6 ppt salinity, young roach (*Rutilus rutilus*) were more abundant in littoral areas with lower salinity. During its first weeks of life, age-0 perch fed in open water, but at about 25 mm total length they changed their habitat to areas with low water depth.

Calculating daily food consumption of fish by bioenergetics models (Kitchell et al., Vinberg, Kerr & Dickie) and by direct measurement during 24 hours, it was found that ingestion of prey species never exceeded the daily production rate of the zooplankton. Consequently, it was concluded that the predation influence of age-0 fish on the population collapse of *E.affinis* yearly observed in late spring was negligible. Additionally, competition for food was assumed to be not a structuring factor within the community of 0+ fish species.

# Spatial and Temporal Dynamics of Phytoplankton Assemblages in Tidepools: Effects of the Physical Environment, the Nutrient Regime and the Grazer Field

**Metaxas, A. 1994**
**Dalhousie University (Canada), 296 pp.**

Tidepools are a potentially significant component of the rocky intertidal environment because they provide a refuge from extreme environmental fluctuations and, therefore, extend the vertical limits of the biological assemblages that inhabit this environment. Also, planktonic organisms are present in pools at all times, as opposed to only at high tide over the emergent substratum. Tidepools are potentially useful systems in which to test general ecological theories because they have well-defined boundaries and can be relatively easily manipulated. However, unlike the emergent substratum of the rocky intertidal environment, little is known about tidepool community structure and organization. Microalgae are important primary producers that are introduced into tidepools through tidal input; over the period of isolation of the pool, they can remain suspended, sink to the bottom of the pool and/or be consumed by filter-feeders or benthic grazers. My thesis examined the temporal and spatial dynamics of phytoplankton assemblages in tidepools, in three intertidal zones on an exposed rocky shore, near Halifax, Nova Scotia, Canada. The dynamics of these assemblages were examined within the tidal isolation period of the pools (short-term temporal scale) and, at monthly intervals, over a period of 16 months (long-term temporal scale). Changes in phytoplankton abundance were related to biotic (e.g. macroalgae, macrofauna, planktonic and benthic micrograzers) and abiotic (e.g. nutrients, temperature, salinity, pH, exchange rate, pool dimensions) factors that may regulate the assemblages.

Changes in phytoplankton abundance within the isolation period of the pools (short-term) were examined at a period of low phytoplankton abundance and during the phytoplankton fall bloom in the surrounding sea-water. Taxon- and date-specific changes in phytoplankton abundance were attributed to grazing effects. The variability in the chemical and physical environment did not explain the few recorded changes in phytoplankton abundance. Between sampling dates, the abundance of most taxa (but not total phytoplankton) was significantly altered, suggesting a shift in dominance. Over the longer temporal scale, there was little indication of vertical zonation of the phytoplankton assemblages along the intertidal gradient, and differences among zones rarely explained more than 30% of the spatial variability in phytoplankton abundance. However, the abundance of all groups of phytoplankton varied significantly among pools within intertidal zones on most sampling dates, and differences among pools explained up to 96% of the variability in phytoplankton abundance. Furthermore, there was significant variability among pools within zones for all biotic and abiotic characteristics of the pools on most sampling dates. In separate studies, I showed that there also was large variability among pools within intertidal zones in the structure of the macrobenthic and hyperbenthic assemblages. In factorial field manipulations, I examined bottom-up (nutrient availability) and top-down (grazing) effects on the composition of phytoplankton assemblages in tidepools. There were no significant bottom-up or top-down effects on any phytoplankton group in experiments conducted in November 1992 or June 1993. Although there was some variability among pools, both a reduction in grazer density and nutrient enrichment had a positive effect on some groups of phytoplankton but a negative effect on others in experiments conducted in July and August 1993.

The results of my thesis suggest that the factors that regulate the temporal and spatial dynamics of phytoplankton assemblages in tidepools probably operate at the scale of the individual pool rather than the intertidal zone. The mechanisms of community regulation in tidepools differ from those on emergent substrata of rocky shores, probably due to differences in the tidal influence on the two habitats.

# Ecology of a Temperate Coral

**Miller, M.W. 1994**
**University of North Carolina at Chapel Hill, 157 pp.**

The general restriction of hard corals and coral reefs to tropical latitudes has been suggested to result from latitudinal variation both in physical (temperature and nutrient/turbidity regimes) and in biotic factors (especially variation in the outcome of competition between hard corals and seaweeds). The following studies represent the first rigorous experimental analysis of the effects of physical factors and of seaweed competition on a temperate coral, *Oculina arbuscula.* Also, latitudinally-varying environmental factors of grazing and nutrient levels were manipulated to discern their role in mediating coral/seaweed competition in warm temperate communities of North Carolina where *O. arbuscula* occurs.

*Oculina arbuscula* showed broad tolerance to temperatures between 8 and 28°C and significantly higher growth in warm than in cold temperature conditions, though growth under cold temperatures was still positive. In microcosms, both light and a zooplankton food supply significantly increased coral growth and chlorophyll a concentration in the coral tissue. In a field experiment with potential competitors removed, corals grew significantly better and had higher chlorophyll concentrations at shallow than at deep depth. Field sampling, however, showed coral abundance to be concentrated in deep, not shallow, habitats. Also, both within and among reef sites, coral distribution was negatively associated with seaweed abundance.

At two sites, corals transplanted into seaweed dominated areas grew well if seaweed canopies were removed but poorly, or not at all, if canopies were left intact. Seaweeds also inhibited *Oculina* recruitment at the turbid, inshore site. At a turbid nearshore reef, cage exclusion of large grazers significantly enhanced recruitment, but this difference could not be attributed to grazer effects on seaweeds. Facilitation was apparently due to consumers removing barnacles, which dominated this low-light site if grazers were excluded.

Cage exclusion of large herbivores (primarily fishes) at two offshore and one inshore site had no significant effect on coral growth. Grazers did alter seaweed species composition at the inshore site(palatable red algae replaced the grazer-resistant brown algae that dominate in the presence of grazers) but had little effect on total seaweed abundance. In contrast, in a simultaneous manipulation of grazing rates and nutrient levels, cages significantly reduced coral growth. Nutrient addition had no effect on brown seaweeds, increased cover of red seaweeds in exclusion cages, and tended to suppress coral growth in full cages where reds were stimulated, but to increase coral growth in open cages where herbivores had removed the red seaweeds. These results suggested that red and brown seaweeds may experience differential levels of nutrient limitation and exert differential competitive effects on coral in this temperate reef system.

These results show that seaweeds exert significant competitive effect on *Oculina*, play a large role in excluding *Oculina* from well-lit temperate reefs, and support the hypothesis that seaweed competition may interact with latitudinal changes in physical parameters to limit corals at high latitudes.

# The Role of Infaunal and Epifaunal Suspension Feeding Macrofauna on Rates of Benthic-Pelagic Coupling in a Southeastern Estuary

**Miller-Way, C. 1994**
**Louisiana State University, 203 pp.**

This research investigated the effects of two suspension feeding bivalves, the infaunal clam *Rangia cuneata*, and the epifaunal oyster *Crassostrea virginica*, on benthic-pelagic coupling in Fourleague Bay, a river-dominated estuary in southeastern Louisiana. A continuous-flow microcosm system was developed to overcome recognized limitations of batch methodology and to facilitate manipulations designed to investigate the ecological role of benthic macrofauna. Experiments comparing traditional batch methodology to continuous-flow methodology indicated that rates of benthic processes were consistently greater when measured using continuous-flow methodology. Concentration changes over time indicated that differences were due to concentration gradients which departed from ambient conditions in the batch cores.

Over an annual cycle, both suspension feeding species significantly increased rates and altered patterns of benthic exchange of both particulate and dissolved materials. Both species increased the retention of particulate material via their filtering activities. Both species significantly increased rates of benthic $O_2$ consumption. Both species released $NH_4$ and $PO_4$ to the surrounding water via their metabolic activity which resulted in increased rates of sediment release or a change in the direction of benthic flux. The magnitude of the change relative to ambient sediment rates varied with season and with the faunal community. Weight - rate regressions indicated that increases were accounted for by individual bivalve metabolism in most cases. Temperature control of physiological processes resulted in maximum rates in summer (*Rangia cuneata*) or fall (*Crassostrea virginica*), while minimal rates occurred during winter for both species. Increases above ambient sediment exchange rates were significantly greater for the oyster than the rangia clam during all seasons except winter. Seasonal variation in weight-specific rates of *Rangia cuneata* was significantly lower than that for the oyster, accounting for the former result. Changes in benthic exchanges caused by the clam were primarily quantitative in nature; rates were increased but nutrient transformations were not altered. In contrast, changes due to the oyster were quantitative and qualitative; fluxes were increased and nitrification was enhanced. The effects of both species on benthic processes resulted in significant changes in stoichiometric ratios when compared to those of the sediment alone, potentially ameliorating water-column phosphate and nitrogen limitation at different times of the annual cycle. Differences between the effects of these species were not entirely due to differences in their respective functional group; results suggested a need for the inclusion of a relative measure of metabolic activity when predicting a species effect on its environment.

A framework, in the form of a dynamic simulation model, was developed in order to evaluate the ecological significance of altered rates and patterns due to the presence of benthic fauna. Increased rates were evaluated relative to other nutrient sources and sinks in the ecosystem. Model simulations addressed the influence of the oyster community on $NH_4$ distributions in the lower Fourleague Bay. Results indicated that riverine input was the primary determinant of observed $NH_4$ distributions in the spring, while in fall, the release of $NH_4$ by the oysters was the most important factor determining water-column concentrations. As primary production rates peak in this area of the bay in the fall, it was suggested that the oyster community plays the primary role in supporting these high production rates.

# Primary Production Dynamics and Trophic Importance of Epiphytic Algae in Mississippi Seagrass Beds

**Moncreiff, C.A. 1993**
**Mississippi State University, 272 pp.**

Primary production rates of four autotrophic components in *Halodule wrightii* Aschers. beds off Horn Island in Mississippi Sound were measured over an annual cycle. Hourly production rates varied from 0.9 mg C $m^{-2}$ for *H. wrightii* leaves to 1143 mg C $m^{-2}$ for epiphytic algae. Stepwise multiple regression showed that only 15% of the variation in hourly epiphytic algal production could be related to a single environmental variable, light energy. Variations in production rates for the other components were best explained by light energy, water temperature, tidal range, and blade density; $R^2$ for these regressions was 0.66 and 0.80 for phytoplankton and seagrass blades, respectively. The epiphytic algal assemblage on *H. wrightii* was dominated by the red alga *Acrochaetium flexuosum* Vickers and 12 taxa of araphid, monoraphid, and biraphid diatoms. Phytoplankton were primarily centric diatoms; the microflora associated with the sandy sediments in which *H. wrightii* was rooted was dominated by small pennate diatoms. Annual production rates (g C $m^{-2}$) were estimated as follows: epiphytic algae (905), phytoplankton (468), sand microflora (339), and H. wrightii (256). System production was dominated by the microalgae; the contribution of *H. wrightii* blades was only 13% of the total. Epiphytic algae were the most productive component, responsible for 46 and 60% of total system and benthic production, respectively.

Multiple stable isotope analyses were used to examine food web dynamics in this seagrass system. Stable isotope ratios for carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) were measured on material collected from May 1989 through November 1992. The $\delta^{13}C$ and $\delta^{34}S$ values of most consumer organisms sampled clustered near those measured for epiphytes, macroalgae, and plankton, rather than the seagrass blades. Trophic levels, as determined by $\delta^{15}N$, were not separated. Stable isotope data, in combination with high measured rates of primary production, strongly suggest that epiphytic algae are the major source of organic carbon for higher trophic levels in this system. The contribution of *H. wrightii* appears to be minimal, at best. The overall picture that is emerging based on the present and previous studies is one of the major trophic importance of benthic microalgae (i.e. epiphytes and sediment-associated microflora) in coastal food webs.

# The Physical Basis of Prey Capture by Heterotrophic Marine Nanoflagellates

**Monger, B.C. 1993**
**University of Hawaii at Manoa, 178 pp.**

Heterotrophic nanoflagellates comprise an important consumer group within pelagic food webs and play a vital role in cycling carbon and nitrogen in the world's oceans. Most primary production passes either directly or indirectly through heterotrophic nanoflagellates in the open ocean. Oceanic nanoflagellates generally have a simple, smooth form and capture their picoplankton-size prey by chance contact with their cell surface as they swim randomly through the fluid medium. In theory, this feeding mechanism does not involve the structural complexity, inter-taxonomic variability, or obvious behavioral complications of higher organisms. Consequently, it may be possible to understand a great deal about this ecologically important trophic interaction by viewing it from a purely physical perspective.

Prey capture by marine nanoflagellates is formulated in terms of physical forces arising between nanoflagellates and picoplankton prey as they approach one another. A numerical model developed to study colloidal interactions is adapted to make predictions of nanoflagellate grazing rates. Predictions are formulated as a function of prey size, nanoflagellate swimming speed and the resultant of a balance between hydrodynamic, London-van der Waals, electrostatic and solvation forces.

In short, the relative strengths of attractive or repulsive molecular and hydrodynamic forces determine nanoflagellate grazing rates on picoplankton prey of a particular size. One of the more significant model predictions is that nanoflagellate grazing rates should increase approximately linearly with prey diameter -- a relationship that conflicts with previously published quadratic and cubic dependencies. Experiments aimed at resolving this discrepancy provides support for a linear size dependency.

The model ignores post-contact rejection of prey. If selective prey rejection occurs to a significant extent, a random contact model of the kind described here would be unreliable for studying natural systems that contain variable prey types. To test for selection based on factors other than size, ingestion rates are compared for a chrysomonad population feeding on different species of live or heat-killed bacteria, *Synechococcus* sp., and latex microspheres. Results indicate that post-contact prey rejection is not significant for this organism. Results from this work also suggested that highly motile bacteria may experience significantly greater predation losses due to an increase in the encounter rate with nanoflagellates.

All grazing rate predictions are low by a factor of 3 or 4 when compared with well-accepted literature values. Varying modeled London-van der Waals and electrostatic double layer forces within reasonable natural limits caused predicted grazing rates to change by less than a factor of two. This led to a reexamination of the importance of the hydrophobic interaction force -- neglected in the current model. Experiments designed to directly measure the effect of the hydrophobic force on grazing rates show that a modest increase in prey-surface hydrophobicity, as revealed by hydrophobic interaction chromatography, can triple the rate at which prey are ingested by nanoflagellates. This result may explain the discrepancy between model predictions and observations of the absolute magnitude of nanoflagellate grazing rates.

# The Relevance of Feeding Environment to "Retention" of Atlantic Herring (*Clupea Harengus*) Larvae

**Muelbert, J.H. 1994**
**Dalhousie University (Canada), 152 pp.**

Despite the economic importance of herring fisheries and several years of intensive research, proximate causes for variability in the recruitment of herring remain unclear. In this thesis, the feeding environment of herring larvae from the coastal waters off SW Nova Scotia is evaluated and discussed in the light of current hypotheses that attempt to explain variable survival during the early life history of pelagic fish.

Throughout the North Atlantic, fall-spawned herring larvae predominantly inhabit coastal regions with tidally well mixed waters. Data from two cruises confirm that large aggregations are confined to well mixed waters off SW Nova Scotia. Physical-behavioural interactions could contribute to this pattern. The diel periodicity of vertical migration exhibited by the larvae, however, is not sufficient to ex-plain the maintenance of their horizontal position through interaction with semi-diurnal tidal current. Alternatively, lower prey abundance in stratified waters could lead to increased mortality from starvation and account for the observed spatial distribution of the larvae. Results show that larvae in well mixed and stratified regions off SW Nova Scotia were exposed to similar concentrations of microzooplankton. Thus, variation in food concentration alone is not sufficient to explain the maintenance of the aggregations in the well mixed region.

It has frequently been suggested that relative motions of predator and prey influence the feeding rate of planktonic organisms. Dimensional analysis of relevant biological parameters describing herring life history and field data shows that tidally well mixed regions constitute a preferential feeding environment for herring larvae because turbulence enhances predator-prey encounter rates. Hence, feeding rates should be greater in well-mixed regions as compared to stratified regions with similar food abundance. Indeed, measurements of RNA/DNA ratios indicate that larvae from the well-mixed areas were healthier than those from stratified areas, and had similar condition throughout the water column. However, larvae from both regions were generally in good condition, supporting the initial finding that during the fall, food is adequate for larval growth throughout the coastal zone.

This thesis supports the hypothesis that tidal mixing enhances the feeding environment of herring larvae. Furthermore, it indicates that as food availability decreases towards the winter, larvae in stratified waters may be more susceptible to starvation. Therefore, differential mortality between the two regions may be the proximate cause for the apparent retention of larvae during winter in the well mixed waters of SW Nova Scotia.

# Modelling Investigations of Marine Microplankton Ecology

**Murray, A.G. 1993**
**University of Southampton (United Kingdom), 387 pp.**

Since the late 1970's increasing interest in the role of bacteria, protozoa and small phytoplankton in pelagic marine ecology has resulted in a new food web paradigm by which nanoplankton (2-20 μm) and picoplankton (0.2-2 μm) account for a large proportion of primary and secondary production. Bacteria assimilate dissolved organic matter (produced by phytoplankton exudation and zooplankton 'messy feeding') and flagellate protozoa graze upon the bacteria and picophytoplankton. Ciliates consume zoo- and phyto- flagellates and are in turn grazed on by crustacean zooplankton. This bacteria-protozoa food chain has become known as the 'microbial loop'.

The purpose of this study is to asses by modelling, the importance of the microbial loop as a carbon salvage pathway for mesozooplankton relative to direct grazing on net phytoplankton. The modelling process demonstrates the quality of existing data on marine microbial ecology and so the model's description transcends a simple methods section. The model divides organisms trophically and metrically and contains manifold time and depth intervals, allowing simulation of variation in microbial ecology to an unprecedented degree. Both carbon and nitrogen cycles are modelled and a $^{14}C$ label can be included. The model "standard run" is shown to be stable over many years and to recover from perturbation. Sensitivity analysis has been carried out for spring and summer periods.

In the model, picoplankton, though productive, play a relatively minor role in mesozooplankton nutrition thus supporting the 'sink' hypothesis. However when nutrients are limiting, both bacteria and picophytoplankton out compete other phytoplankton thereby enhancing the relative role of the microbial loop. Nanozooflagellate grazing releases much of the picoplankton nutrient uptake. Nanophytoplankton are an important indirect food source for mesozooplankton via the microzooplankton, except in winter. The model shows considerable seasonal and spatial variation in community structure, and small diurnal changes. When applied to three differing environmental regions of the North Atlantic by varying initial winter nutrient and total irradiance levels the model results are generally in agreement with reported environmental observations.

# The Role of Dimethylsulfoniopropionate (DMSP) in Marine Macroalgae of the Montery Bay.

**Nishiguchi, M.K. 1994**
**University of California at Santa Cruz, 232 pp.**

Global sulfur cycling in oceanographic systems is an important process for understanding the control and regulation of biogeochemical processes in the world today. A number of marine algae, phytoplankton, and seagrasses produce high amounts of sulfur based compounds which chemically influence the marine environment. One particular solute, dimethylsulfoniopropionate (DMSP), is found in high concentrations and is closely linked to global oceanic sulfur cycles. The conversion of DMSP into dimethylsulfide (DMS) is catalyzed by an enzyme called dimethylpropiothetin dethiomethylase (DMSP lyase). The regulation of DMSP conversion and the biochemical pathways involved in this cycling are not well understood. This thesis project experimentally compared the different pathways of DMSP degradation from several species of macroalgae to elucidate what factors influence the production of DMS into oceanic environments.

Analysis of the macroalgal enzyme, DMSP lyase was performed, and the isolation, purification, and characterization was completed on the Rhodophyte *Polysiphonia paniculata* (Montagne). These experiments demonstrated how DMSP lyase is a key enzyme for the production of DMS from this marine macrophyte. A polyclonal antibody was made to the purified protein, and a cDNA library was made to identify the DMSP lyase gene. Positive results from Northern and Southern hybridizations from species of algae having DMSP lyase activity indicate that the DMSP lyase enzyme is conserved throughout many genera of algae.

The growth of several DMSP producing algae and the enzyme kinetics of each algal DMSP lyase was monitored from specimens in laboratory cultures grown at different salinities. Algal species which produced large amounts of the DMSP lyase enzyme and had better growth rates at higher salinities than other species without the enzyme.

Specimens of the Chlorophycean algae *Ulva taeniata* and *Ulva angusta*, along with *Polysiphonia paniculata* were examined for the production of DMS with and without their natural abundance of epiphytic bacteria. Field collected *Ulva* species had a noticeable difference in DMS production compared to laboratory-reared cultures. The bacteria were isolated and characterized using molecular techniques, and group-specific assays did not determine whether the epiphytic bacterial communities associated with various macroalgae differ between DMSP and non-DMSP producing algae.

# Study of Zooplankton in Two Mediterranean Coastal Lagoons: The Estany of Cullera and the Albufera of Valencia (Spain)

**Oltra, R. 1993**
**University of Valencia (Spain), ?? pp.**

The study of zooplankton in two coastal lagoons, Estany of Cullera and Albufera of Valencia (E, Spain), were carried out between October 1980 to August 1982 and between July 1982 to July 1983, respectively.

The Estany of Cullera is a meromictic coastal lagoon with an anoxic monimolimnion of sea water and a mixolimnion of continental oligohaline water. During the time of study a fluctuating halocline between 1 to 3 m of depth and an oxycline between 3 to 5 m was recognized. Seventy-eight zooplankton taxa (8 marine taxa) were identified, with a mean biomass and zooplankton density of 3.6 g $m^{-2}$ and 1368 x $10^3$ indiv. $m^{-2}$ (63.9% rotifers, 18.6% copepods, 12.2% protozoans, 3.9% polichaetes and 1.3% cladocerans), respectively. The most abundant species were: (1) *Brachionus calyciflorus*, *Brachionus angularis*, *Asplanchna brightwelli*, *Polyarthra vulgaris-dolichoptera*, and *Notholca salina* in the oligohaline surface waters; (2) *Acanthocyclops robustus*, *Metacyclops minutus*, *Moina micrura* and *Synchaeta tremula* between the halocline and the surface; (3) *Calanipeda aquae-dulcis*, *Brachionus plicatilis*, *Synchaeta oblonga* and *Hexarthra oxyuris-fennica* in the halocline; (4) the marine species *Synchaeta grimpei*, *Mercierella enigmatica* and *ciliates Euplotidae* in the halocline or below it. Despite these differences in the vertical profile, seasonal succession is the most important cause of variation of the species density and composition.

The Albufera of Valencia is a hypertrophic lagoon with mean conductivity and chlorophyll *a* concentration of 2335 =B5S $cm^{-1}$ and 400 =B5g $l^{-1}$, respectively. Thirty-two zooplankton taxa were identified, with a mean biomass and zooplankton density of 3.24 mg $l^{-1}$ and 2076 indiv. $l^{-1}$ (77% rotifers, 22.8% copepods, 0.2% cladocerans), respectively. The most abundant species was the permanent copepod *A. robustus* and the rotifer *B. angularis* (with maximums of up to 12,000 indiv. $l^{-1}$ in summer). Other abundant species were *M. micrura*, *B. plicatilis*, *B. calyciflorus*, *Asplanchna girodi* and *Polyarthra* spp. in summer; (2) *S. oblonga* and *B. urceolaris* in autumn; and (3) *Daphnia magna* and *Brachionus leydigi* in spring. The species *B. calyciflorus*, *B. urceolaris* and *M. micrura* were more abundant at the northern stations with less density of cyanobacteria.

# The Effects of Near-Bed Hydrodynamics on Benthic Bivalve Filtration Rates

**O'Riordan, C.A. 1993**
**Stanford University, 279 pp.**

Predictions of phytoplankton depletion by benthic bivalves in shallow, tidally driven estuaries must account for the formation of concentration boundary layers near the bed. These regions of low phytoplankton concentration result from the dynamic interactions of bivalve siphonal currents (excurrent jets and incurrent sinks) with the overlying turbulent boundary layer. To study the near-bed hydrodynamics of the benthic boundary layer, we conducted controlled experiments with the species *Tapes japonica* and *Potamocorbula amurensis*. Two different sets of experiments were conducted in two laboratory flumes, one with model clams and one with live animals.

Using multiple jets and sinks to represent bivalve siphonal currents, model experiments were performed to study the mixing characteristics of phytoplankton-depleted fluid. PLIF (Planar Laser Induced Fluorescence) and LDV (Laser Doppler Velocimetry) were used as the main diagnostics to characterize respectively the concentration and velocity fields. Refiltration fractions were determined by monitoring the concentration of dye ingested by incurrent siphons. Results show that refiltration fractions can be as high as 48%, and are a function of several dimensionless parameters: animal spacing, $S/d_O$, velocity ratio, $VR=u_j/U_\infty$, siphon height, $h_S/d_O$, and crossflow Reynolds number, $Re_x$, based on the distance from the boundary layer trip, x. (S is the mean distance between animals, $d_O$ is the excurrent siphon diameter, $h_S$ is the animal siphon height, $u_j$ is the excurrent jet velocity, and $U_\infty$ is the freestream velocity.) We found that a good estimate of refiltration, n, based on animal spacing, is $(n\ S/d_O) \approx 2\text{-}3$. Differences in concentration profiles calculated from PLIF images for different flow conditions are likely due to the relative influence of four sources of turbulence in the flow: boundary layer shear, boundary roughness, jet in a crossflow, and multiple jet interactions.

Results of experiments with live animals indicate that the presence of actively feeding bivalves causes a velocity defect region close to the bed in the longitudinal velocity profile. The results of live animals observations are used to validate the assumptions used in the design of the model clams and to describe feeding behavioral responses to changes in crossflow velocity. Finally, implications for field observations of concentration boundary layer formation are discussed and our refiltration results are incorporated into a conceptual mass-balance model for food depletion at the bed.

# Mechanisms Controlling the Relative Abundances of Three Suspension Feeding Calanoid Copepods in Dabob Bay, Washington

**Osgood, K.E. 1993**
**University of Washington, 136 pp.**

The abundances and distributions of the marine planktonic copepods *Calanus marshallae*, *Calanus pacificus*, and *Metridia lucens*, along with some of the factors controlling them, were investigated in Dabob Bay, a fjord in Washington. *C. pacificus* copepodids were closely associated with the surface waters, either displaying a normal diel vertical migration (DVM) or being nonmigratory. *M. lucens* copepodids were less strongly associated with the surface layers and their migration behavior was more varied. Some stages displayed normal DVM, some did not migrate, and others displayed reverse DVM at times. On most dates there were significant portions of all stages of *M. lucens* in the deepest layers sampled.

The life histories of *C. marshallae*, *C. pacificus*, and *M. lucens* were determined. *C. marshallae* emerged from diapause and moulted to adults in January and February. One major generation was produced, mainly during early to mid-March. Most surviving individuals spawned in March, arrested development at the C5 stage and were in diapause by late May. *C. pacificus* emerged from diapause and produced its first spring generation slightly after *C. marshallae* and produced additional generations in the late spring and the fall. By mid-fall the population was dominated by diapausing C5s. *M. lucens* did not appear to enter a diapause state. The fall and winter populations were chiefly adult females which demonstrated some activity. *M. lucens* produced generations in late winter/early spring, late spring, and late summer/early fall.

Predation and advection acted to differing degrees on all three populations, changing their abundance cycles from those expected based on the life histories. All three species had major reproductive periods in spring, but only *M. lucens* consistently increased in abundance at this time. This was likely because the vertical distributions of *M. lucens* copepodids make them less available to predators and less susceptible to wash-out from the bay. *C. pacificus* appeared most influenced by predation and advection. Its numbers in fact decreased during spring reproductive periods, but increased dramatically during the fall reproductive period. However, the fall increase appeared largely due to advection of overwintering individuals into the bay.

# A Taxonomic, Ecological and Commercial-Potential Study of the Genus *Gracilaria* (Glacilariaceae, Rhodophyta) of the Kenya Coast

**Oyieke, H.A. 1993**
**University of Nairobi (Kenya), 281 pp.**

A study was conducted on the taxonomy, ecology, and yield, as well as properties of polysaccharides, of the marine algal genus *Gracilaria*. Eight species (*G. corticata, G. crassa, G. edulis, G. fergusonii, G. milladertii, G. salicornia, G. verrucosa* and *Gracilaria* sp.) were identified and reported both from intertidal as well as sublittoral zones. Of the eight species studied, *G. corticata* and *G. salicornia* were the most variable morphologically, depending on prevailing physiological and ecological conditions. With respect to their distribution along the coast, *G. salicornia* was the most common followed by *G. corticata* and *G. crassa*. Studies on their seasonality showed a general single growth peak for the genus, between the months of September and December.

Based on their availability in adequate quantities, six species (*G. corticata, G. crassa, G. milladertii, G. salicornia, G. verrucosa* and *Gracilaria* sp.) were investigated for their agar yield and quality. The effects of morphotypes, habitats and seasons on the quality and quantity of agar extracts were studied. Native agar yields from hot water extracts ranged from 8.1% - 30.3% dry weight, with *G. verrucosa* and *G. salicornia* yielding the highest and lowest amounts respectively. From 1.5% solutions of native agar the highest gel strength was recorded from *G. verrucosa* (220 g $cm^{-1}$), also having the highest content of 3, 6 anhydrogalactose (23%). On the other hand, extracts from *G. corticata* gave the lowest gel strength (<60 g $cm^{-2}$) and the lowest 3, 6 anhydrogalactose content (14.5%). Other chemical and physical properties of the extracts, such as melting and gelling temperatures, sulphate contents, and effects of alkali treatment, were also studied.

Implications of the results obtained from this study are discussed with respect to seaweed farming in the Kenyan waters. Considering their agar yield and quality, G. verrucosa and G. crassa are recommended for further culture experiments, which were beyond the scope of this study. These two species are viewed as possible candidates for commercial food agar production if they can successfully be cultivated on a large scale.

# Distribution, Dynamics and Controlling Processes of Planktonic Bacteria in the Upper St. Lawrence Estuary

**Painchaud, J. 1994**
**University of Laval (Canada), 121 pp.**

The objective of this thesis was to elucidate the role of biological and physical processes in the control of the distribution of planktonic bacteria in the upper St. Lawrence estuary. In the first chapter, the growth response of freshwater bacteria from the St. Lawrence River, exposed to brackish waters (S = 0-20) from the upper estuary, was assessed with the combined use of dilution cultures and diffusion chambers. Growth of the freshwater bacteria was reduced by 15% and 50% after exposure to salinities of 10 and 20, respectively. At lower salinities, no growth reduction was observed and at S = 2, growth was even stimulated. In contrast with an earlier hypothesis, the present study shows that the decline of bacterial abundance in the low salinity waters of the estuary is not caused by salinity-related mortality of freshwater bacteria, because mixing time between fresh and marine (S > 20) waters is relatively long (days). However, the results suggest that salt-induced mortality can be an important process in estuaries with shorter mixing times (hours). The combined use of diffusion chambers and dilution cultures proved to be a useful methodology for assessing growth (or mortality) of bacteria along environmental gradients.
The second chapter analyzes the spatial distribution and semi-diurnal variability of bacteria at six stations in the upper St. Lawrence estuary. Free and attached bacteria showed different patterns of spatial distribution and variability. Free bacteria exhibited highest mean concentrations in freshwater (3.5-4.4 $10^6$ $ml^{-1}$) and lowest concentrations at the downstream stations (0.3-0.5 $10^6$ $ml^{-1}$); their numbers declined exponentially relative to salinity. Attached bacteria had highest mean concentrations (3.2-5.5 $10^6$ $ml^{-1}$) near the head of the estuary, at salinities between 0.5 and 5 and were virtually absent at downstream stations (< 0.05 $10^6$ $ml^{-1}$). The analysis of causal models between salinity, and free and attached bacteria, showed that the two types of bacteria are uncoupled and that both types have a strong relationship with salinity. Physical processes are, thus, important controlling factors of the distribution and variability of bacteria. Results suggest that large-scale processes, such as fresh water outflow and residual circulation, largely control free bacteria, whereas short-term and more local processes (e.g. sediment resuspension caused by wind) may also be important in the control of attached bacteria.

In the third chapter, the distribution of free bacteria in the upper St. Lawrence estuary was interpreted using bacterial fluxes and residence times, derived from a circulation model, and growth/grazing rates determined using cultures. Bacterial abundances decreased exponentially along the salinity gradient, from 3.9 x $10^9$ $l^{-1}$, in fresh water, to 0.5 x $10^9$ $l^{-1}$ at S > 20. Rates of growth and grazing were of the same order of magnitude (0.02-0.08 $h^{-1}$ and 0.01-0.09 $h^{-1}$, respectively), which suggests that bacteria tended towards a state of trophodynamic equilibrium (growth ≈ grazing). Negative bacterial fluxes show that the estuary is a sink for bacteria. Net production/predation values, calculated from rates of growth/grazing and bacterial concentration, are consistent with flux values, which confirms the validity of cultures and circulation model. Results suggest that the longitudinal distribution of bacteria is largely under hydrodynamic control and point to predation as the process causing bacterial losses in the estuary. Rates of dispersion and growth/grazing are of the same order of magnitude, whichs shows that biological processes are nevertheless significant relative to physical processes. Data lead to the following conclusion: although free bacteria are largely under hydrodynamic control, they should not be regarded as a conservative variable, because significant biological rates and transformations are observed within the bacterial community during estuarine transit. This study demonstrates the importance of quantifying and, in particular, setting the temporal scale of the processes underlying distributions, instead of using approaches restricted to the analysis of state variables.

# Chlorophyll *a* Spatial Microstructure Determination from Volumetrically Reconstructed Optical Serial Sectioned Fluorescence Images

**Palowitch, A.W. 1994**
**University of California at San Diego, 139 pp.**

Knowledge of the spatial and temporal variability of the optical properties of coastal and oceanic waters has important applications in biological and physical oceanography. On a sub-meter scale the variation in absorption, scattering, and fluorescence properties indicates the distribution and interaction of biological particles and the effects of internal waves, currents, and localized density differences. In a demonstration of the capability to determine microscale phytoplankton distributions, an underwater serial sectioning tomography technique which measures induced Chlorophyll *a* fluorescence has been developed. The technique involves scanning a 457 nm illumination plane through a range of distances parallel to the imaging plane of a $1024^2$ pixel digital CCD camera. Images of induced fluorescence at 685 nm in the sequentially illuminated planes are recorded. A theoretical model of the imaging process in the form of $\mathbf{i} = \ln \mathbf{c} + \mathbf{Ac} + \mathbf{x}$ shows that the image, **i**, is a function of a spatially varying **c** (Chl *a*) - dependent absorption component **A**, and a spatially invariant attenuation component, **x**. A numerical inverse method, incorporating an environmentally dependent calibration constant, is used to calculate Chl *a* values from the image intensities for three dimensional presentation. A stable reconstruction, not affected by noise induced error propagation, was demonstrated. Laboratory testing of a prototype system has shown that Chl *a* concentrations from 0.1 to 2.0 mg Chl *a* / $m^3$ at a 0.1 mg Chl *a* / $m^3$ resolution can be determined. The limiting factor in the imaging process is the rapid attenuation of the fluoresced 685 nm light which determines the system optical depth, $\xi$. With 0.1 mg Chl *a* / $m^3$ as a minimum, $\xi = 0.97$. At this $\xi$ and $c_{(685)} \leq 0.7$ $m^{-1}$, a 1 $m^3$ volume of 0.1 mg Chl *a* / $m^3$ can be imaged with a spatial resolution of 1 $cm^3$. At higher Chl *a* levels larger values of $\xi$ permit larger volumes to be imaged. The remote sensing aspect of this underwater tomography technique permits in-situ Chl *a* microstructure information to be obtained without disturbing the naturally occurring phytoplankton distributions.

# Production of Domoic Acid, a Neurotoxin, by the Diatom *Pseudonitzschia Pungens* F. *Multiseries* Hasle under Phosphate and Silicate Limitation

**Pan, Y. 1994**
**Dalhousie University (Canada), 245 pp.**

*Pseudonitzschia pungens* f. *multiseries* Hasle is the first diatom to have been implicated in an episode of shellfish poisoning. In 1987, 150 people became sick and three died after consuming mussels, *Mytilus edulis*, from Cardigan Bay, Prince Edward Island (Addison and Stewart, 1989). It was discovered that the mussels had been feeding on a monospecific bloom of *P. pungens* f. *multiseries*, and the toxin involved was domoic acid (DA, Subba Rao *et al.*, 1988a). This thesis reports an investigation of the physiology of the diatom, with particular emphasis on factors that lead to DA production.

Photosynthesis, phosphate (P) and silicate (Si) uptake, and domoic acid production were studied in batch and chemostat continuous cultures. The photosynthetic carbon assimilation rate of *P. pungens* f. *multiseries* was low compared to other diatoms, especially when the cultures progressed into stationary phase and were nutrient limited. Luxury uptake of P and Si occurred when the culture populations were perturbed with these nutrients after being starved of them. Domoic acid was produced both in dividing and non-dividing populations and the production rates correlated with the severity of P or Si limitation. Production of DA was significantly enhanced when overall cell metabolism declined due to nutrient limitation. In the batch cultures, there were two stages of DA production. The first stage corresponded to the decline of population growth, and the second stage to nutrient limitation. These two stages are believed to be controlled by self-limiting factors and external stress respectively. In continuous culture, the same two stages were detected. Under severe limitation of either P or Si, DA production rose to maximum levels around 200 $\mu g\ l^{-1}\ d^{-1}$ (3.17 pg DA $cell^{-1}\ d^{-1}$) and the maximum DA levels attained were 11.9 pg DA $cell^{-1}$ in cells and 1118 $\mu g\ l^{-1}$ in whole culture. The main conclusions are (*i*) the self-limiting control associated with decline of population growth is an essential prerequisite to DA production, but the main control is external nutrient stress; (*ii*) the major cell mechanism regulating DA production is a change in partitioning of energy and precursors between primary and secondary metabolism; (*iii*) the domoic acid poisoning episodes in Cardigan Bay were likely caused by abnormal nutrient ratios in the sea water.

# A Laboratory and Field Study of Sublethal Predation on the Brittlestar, *Microphiopholis Gracillima* (Stimpson) (Echinodermata: Ophiuroidea), by White Shrimp and Other Macerating Predators: An Immunochemical Approach

**Pape-Lindstrom, P.A. 1994**
**University of South Carolina, 136 pp.**

Predation is a major force controlling community structure. Sublethal predation (e.g., tail and palp nipping of polychaetes, cropping of bivalve siphons, and grazing of brittlestar arms) is one type of energy transfer which is virtually uncharacterized in marine benthic habitats. Worldwide, infaunal brittlestars, with arm regeneration scars documenting past sublethal tissue loss, may serve as a renewable energy resource for benthic predators. Flatfishes, shrimp and crabs are known or suspected predators.

A model system with white shrimp, *Penaeus setiferus*, as the predator and the infaunal brittlestar, *Microphiopholis gracillima*, as the prey was studied to understand and quantitatively assess sublethal predation. Laboratory feeding rate experiments established that white shrimp eat brittlestar arm tissue in large amounts (80 mm shrimp$^{-1}$ h$^{-1}$) when access to brittlestar prey is maximized. Sublethal predation decreased when brittlestars had access to a sediment refuge (22 mm shrimp$^{-1}$ h$^{-1}$). White shrimp consumed arm tissue at the same rate in the presence of an additional food source. The immunochemical survey of gut contents documented a variety of invertebrate and vertebrate predators of the brittlestar in North Inlet, South Carolina: 88% of white shrimp (n = 92), 70% of blue crab (n = 30), and 40% of brown shrimp (n = 23) had ingested brittlestar arm protein. Hermit crabs, spot, and silver perch consumed brittlestars less frequently.

Field experiments, conducted in North Inlet, SC, were the first to yield a daily sublethal predation loss rate for any prey species. A loss rate of 20 mm arm tissue brittlestar$^{-1}$ d$^{-1}$ was measured and converted to grams ash-free dry weight (AFDW) using a regression relating arm length to AFDW. Shrimp abundance data from North Inlet, the daily sublethal arm tissue loss rate and knowledge of the life history of the brittlestar were used to calculate estimates of annual trophic energy transfer due to sublethal predation on the brittlestar community in North Inlet. These values had a range of 3.338-9.737 g AFDW m$^{-2}$ y$^{-1}$, which is equivalent to total secondary production in other benthic environments with similar physical characteristics. This study conclusively demonstrates that sublethal predation on brittlestars and other benthic species can no longer be ignored.

# Effects of Fish on Planktonic Communities and Food Web Response to Varying Predation Pressures and Nutrient Regimes

**Pérez-Fuentetaja, A. 1993**
**State University of New York at Syracuse, 135 pp.**

Two experiments in aquatic mesocosms were undertaken in 1991 and 1992 to assess the impact of fish on planktonic populations and their recovery. Five treatments (n=2) were applied in oligotrophic Wolf Lake (New York): (1) high fish biomass (30 kg/ha), (2) low fish biomass (10 kg/ha), (3) high removal of zooplankton, (4) low removal of zooplankton and (5) control. TP, chlorophyll *a*, zooplankton biomass, and zooplankton species richness decreased from high fish > low fish > control > low removal > high removal treatments. A phosphorus bioenergetic model revealed that fish excretion in the high fish treatments was responsible for the highest levels of TP observed (3.6 times higher than the control). Zooplankton excretion was not a major contributor to the phosphorus pool when fish were present. The main role of fish was to modify nutrient cycling. These results suggest that in oligotrophic systems, planktivorous fish are significant nutrient sources and that bottom-up forces structure the planktonic community.

Six treatments (n=2) were applied to oligotrophic Ranger Lake (Ontario) in a factorial design. Half of the mesocosms were enriched by adding nutrients to double natural lake concentrations. The treatments were: (1) oligotrophic high fish biomass (161 kg/ha), (2) oligotrophic low fish biomass (47 kg/ha), (3) oligotrophic control, (4) eutrophic high fish biomass, (5) eutrophic low fish biomass, (6) eutrophic control. The experiment was divided into three periods: (a) before addition of fish, (b) during fish presence, and (c) after fish were removed. These three periods were compared to evaluate fish impacts and zooplankton recovery. TP and ammonia increased in the fish mesocosms, indicating an effect of fish on nutrient levels. Planktonic communities with low levels of fish were more resistant to changes in density in both nutrient environments. However, the populations in the eutrophic mesocosms recovered faster from fish predation. The most omnivorous group of zooplankton had high levels of interaction and contributed to community recovery. Planktonic populations in the eutrophic mesocosms were more persistent over time. Oligotrophic systems were relatively more dynamic and had ample stability domains. Differential nutrient recycling rates for oligotrophic and eutrophic systems may be the cause underlying the observed recovery rates.

# Hydrodynamic Forcing on Shallow Water Communities: Some Physical Effects and Ecological Consequences of Internal Tidal Bores

**Pineda, J. 1993**
**University of California at San Diego, 158 pp.**

This dissertation develops themes at the interface between ecology and physical oceanography through the consideration of an important physical mechanism: internal tidal bores. Internal tidal bores are shown to account for a wide and disparate phenomenology. This dissertation demonstrates that nearshore physical phenomena that can be explained by internal-tidal bores include: 1) drops in surface water temperature lasting several days; 2) predictability in surface water temperature within the lunar cycle in spring and summer but not in winter and fall; and 3) the onshore translation of warm-water fronts and associated replacement of nearshore bodies of water at diurnal or semidiurnal periodicities. To explore whether large internal-tidal bores were a geographically widespread phenomenon, long time-series of surface water temperature were used; the evidence supports the idea that this phenomenon is common along the western United States. Evidence is presented regarding the biological consequences of internal tidal bores. Water column larvae inhabiting subsurface or thermocline water are transported onshore when subsurface cold water is advected by the internal bores. When the cold, denser water sinks and slides offshore, it is replaced by onshore-moving warmer water; warm-water fronts lead the warm water. It is shown that neustonic larvae are transported onshore in these fronts. Using an historical diatom time-series, some evidence was found for increased abundance of diatoms on the days of the lunar cycle when water is predictably coldest (due to internal tidal bores).

Another study focuses on the correlation between the transport and settlement of larvae and other factors influencing settlement rate. This study suggests that temporal variability in settlement rate at scales of 100 m are related to the larval pool and to physical transport processes, while spatial variability is associated with behavioral response and substrate availability. Evidence is also presented to support the idea that the proportion of unmetamorphosed larvae to total settlement is a periodic, semi-lunar ($\approx$ 14.7 days) phenomenon that is related to restricted immersion times.

Overall, this dissertation presents a parsimonious hypothesis for explaining a previously unrelated array of phenomena. The hypothesis describes a broadly predictable process with profound but largely unexplored implications for nearshore communities.

# Ecology of Intertidal Benthic Microalgal Communities in North Inlet Estuary, South Carolina

**Pinckney, J.L. 1992**
**University of South Carolina, 276 pp.**

Estuarine benthic microalgal communities, composed of a mixed assemblage of benthic diatoms, cyanobacteria, and chlorophytes, inhabit the intertidal and subtidal sediments of coastal systems. Benthic microalgae are a primary carbon source for estuarine food webs, are an important component in nutrient cycles, and function as sediment stabilizers. The purpose of this research was to construct an ecophysiologically-based production model for North Inlet Estuary, SC, USA. The approach was to characterize the habitat-specific properties of benthic microalgae, construct and validate the model, and subject the model to sensitivity analysis to determine the relative importance of model components.

The estuary was divided into a mosaic of 5 habitat types based on sediment type, sunlight exposure, and tidal elevation. Using stratified-random sampling methods, biomass (Chl *a*) and production measurements were obtained from each habitat type at bimonthly intervals during 1990-91. Photosynthetic rates were determined using oxygen microelectrodes and Chl *a* was quantified by HPLC and spectrophotometric methods. Short-term (hourly) variability in production was attributed to vertical migration by benthic diatoms in the upper 5 mm of sediments. A curvilinear regression model revealed that much of the short-term production variability could be attributed to changes in tidal and sun angles. Habitat-specific photophysiological characteristics were assessed using PI curves obtained from benthic microalgal communities in different *in situ* light environments. Based on PI and photopigment characteristics, benthic microalgae appeared to readily photoacclimate to the ambient light environment. The production model, which incorporated the habitat-specific photophysiological and behavioral responses to *in situ* conditions, provided estimates of annual *in situ* benthic microalgal production in each of the 5 habitat types. The main factors in the model were *in situ* irradiance, photophysiological response, vertical migration periodicity, and microalgal biomass. Comparisons of field-based areal ($m^{-2}$) production with model predicted areal production revealed a significant positive correlation ($r^2 = 0.63$) with a slope of 1.0, suggesting that the model provided both accurate and reliable estimates of benthic microalgal production. Annual estimates of habitat-specific production were multiplied by the area of each habitat type to determine total microalgal production for the entire estuary. Short *Spartina* zone habitats provided 58% of the total annual production, followed by intertidal mudflats (21%), tall *Spartina* zones (3%), shallow subtidal (11%), and intertidal sandflat (7%) habitats. The average annual benthic microalgal production for North Inlet estuary in 1990-91 was estimated to be 4079 tonnes C $y^{-1}$. When compared with other estuarine phototrophs, benthic microalgae provide more than one third of the primary production in this estuary.

The spatial distribution of meiofaunal herbivores was compared to the distribution of microalgae using spatial autocorrelation techniques to analyze spatial patterns. Meiofauna and microalgae have nearly identical spatial patterns and similar patch sizes, suggesting a common spatial linkage between meiofaunal grazers and microalgal resources.

# The Role of Sulfur in the Preservation of Isoprenoid Hydrocarbons in Sedimentary Materials of the Washington Continental Margin

**Pinto, L.P. 1993**
**Oregon State University, 220 pp.**

A systematic study of highly branched isoprenoids (HBI) was carried out in suspended particulate material (SPM) and Washington coastal sediments to determine their origin and fate. SPM collected at 10 m depth was filtered through Nitex membranes. $C_{25}$ HBI were found only in the 1.2-40 μm range over the shelf. The particle size fractionation of SPM shows different enrichment for n-heneicosahexaene (HEH), a common hydrocarbon in phytoplankton, and the sum of $C_{25}$ HBI in the finer fractions suggesting these hydrocarbons do not share a common source. The distribution of $C_{25}$ and $C_{25}$ HBI correlates with the chlorophyll maxima suggesting an upper-water microbial source associated with phytoplankton biomass.

It has been hypothesized that sulfur addition into specific biomarkers occurs during the early stages of diagenesis. Incorporation of the HBI into a refractory geomacromolecule via a sulfur linkage or formation of HBI-thiophenes are not evident in the sedimentary lipids. HBI show a rapid decrease in concentration with depth in both midshelf and slope sediments suggesting that biodegradation is the major pathway for their disappearance in Washington coastal sediments.

Sediment cores from a midshelf and slope locations show the existence of suboxic/anaerobic conditions within the first 5 cm in the sediments. Elemental sulfur distribution in the midshelf appears to be controlled by bioturbation. On the slope, its profile indicates a quasi steady state regime.

Phytane and phytenes (∑Phy) are the major products of Raney nickel desulfurization in both midshelf and slope sediments. A strain of the coccolithophorid *Emiliana huxleyi* obtained from the Sargasso Sea and treated with Raney nickel showed a strikingly similar pattern to the desulfurization products of sedimentary lipids. The amount of ∑Phy in the slope decreases abruptly by a factor of 6 in the top 2 cm and gradually increases with depth. These results are interpreted as phytyl coming from two sources: (1) chlorophyll-a and (2) S-bound to geomacromolecules. Partial release of phytyl moieties from chlorophyll-a warrants a reevaluation of Raney nickel as a selective desulfurizing agent before its application for paleoenvironmental reconstruction.

Reducing micro-environments appear to exist within the bioturbated zone in shelf sediments. However, there is no clear evidence for phytyl moieties S-linked to macromolecules within the mixed layer. Results obtained during this study indicate that sulfur incorporation to biomarkers, although present, does not represent a significant mechanism for the preservation of organic carbon in normal marine sediments.

# Experimental Validation of a Model for Biological Nutrient Removal in Activated Sludge Plants

**Pollice, A. 1994**
**Politecnico di Milano (Italy), 284 pp.**

This work is part of a multi-year research program of DIIAR, Politecnico di Milano in the field of eutrophication control by biological nitrogen and phosphorus removal from wastewater, with particular focus on control of nutrient loads ending into the Venice lagoon. The aim of the work was to use experimental data for the first validation of a new mathematical model for biological organic carbon, nitrogen and phosphorus removal from wastewater. The model (developed in 1992 by F. Malpei, DIIAR, Politecnico di Milano) was obtained by merging two existing models (a) for biological organic carbon and nitrogen removal and (b) for biological phosphorus removal in enhanced cultures. It provides the concentration of substrates and biomasses for a number of different wastewater treatment plant configurations, thus allowing to punctually control processes and to predict performances.

Biological wastewater treatments are based on the ability of specific bacterial colonies to utilize organic carbon, nitrogen and phosphorus compounds for their metabolism, thus removing them from the liquid phase. The first part of this work gives a description of the main biochemical and microbiological processes backing biological nutrient removal. Various plant configurations able to improve removal processes by creating the best conditions for the development of specific biomasses are also presented. Bacterial colonies naturally select based on the environment surrounding them, therefore plant configurations are based on different sequencies of anaerobic, anoxic and aerobic bioreactors.The most important steps to understand mathematical models for the simulation of nutrient removal processes are reviewed in the second part. A description of all the different substrates and biomasses taking part in the various processes is also provided, along with an explanation of the processes themselves and their mathematical representation.The third part describes the model to be validated, its rationales, the matrix representation format and the hypotheses sustaining the merge of the two previously existing models.

The report of the experimental program, aimed to collect data for the validation of the model, is presented in the fourth part. A pilot plant (total volume 2 $m^3$) adopting a UCT (University of Cape Town) configuration was installed next to one of the largest plants discharging into the Venice lagoon and treating a mix of industrial and domestic wastewater. The pilot plant treated the same influent sewage of the full scale one and operated for one year. Operations were extensively monitored and a large amount of experimental results were collected. In particular, the last 100 days of operation provided the most suitable data for the model's validation. This last period was divided into four sub-periods, related to the external feed of different concentrations of a readily biodegradable carbonaceous substrate to the pilot plant. Average removal efficiencies for organic carbon, nitrogen and phosphorus were as high as 90%, 70% and 80% respectively. This was achieved despite the extreme variability of the influent concentrations, which varied between 20 and 636 mgCOD/l for soluble organic matter, between 35.7 and 74.5 mgN/l for total Kjeldhal nitrogen and between 4.32 and 60.13 mgP/l for total phosphorus. The fifth part of the work dealt with the utilization of experimental results for validating the model. The latter was expressed as a FORTRAN computer program, installed on a personal computer (80486 processor) and linked with a set of math-libraries. The experimental data were used as parameters and initial values for the iterations leading to the final solution. Eventually, the output of the model (biomass and substrate concentrations in the reactors) was compared with the values observed at the pilot plant. This comparison showed that the calculated results were very close to the measured values, confirming the effectiveness of the model and its suitability for improving treatment plants performances and ultimately control eutrophication in the lagoon.

# Cadmium Accumulation in the Bottom Sediments and Fish of Seepage Lakes in North-Central Wisconsin: Relation to Lake Chemistry

**Powell, D.E. 1993**
**Iowa State University, 126 pp.**

Cadmium was quantified in surficial sediments (uppermost 5 cm) of six lakes in north-central Wisconsin. The lakes are small (8 - 70 ha) seepage basins (no surface inlets or outlets) that spanned a broad range of pH (5.2 - 7.0), acid neutralizing capacity (ANC, -5 - 127 $\mu$eq $l^{-1}$), and dissolved organic carbon (DOC, 1.7 - 6.8 mg $l^{-1}$). A random sampling design, stratified by water depth, was used to select 50 sampling sites in each lake, where sediment samples were collected with diver-operated corers. Dry-weight concentrations of cadmium in the sediments (range 0.02 - 7.17 $\mu g\ g^{-1}$) were significantly ($p < 0.001$) correlated with volatile matter content ($r_S$ ranged from 0.53 - 0.93; Spearman rank order correlation) and water depth ($r_S$ ranged from 0.68 to 0.87) in all six lakes. However, when concentrations were expressed on a volumetric basis (i.e., mass per volume of wet sediment), the positive correlation between cadmium content (range 0.004 - 0.067 $\mu g\ cm^{-3}$) and water depth was significant ($p = 0.05$) for only one of the lakes. Whole-lake burdens of cadmium in the surficial sediment (range: 625 - 5785 g $lake^{-1}$) were strongly correlated ($r_S > 0.99$) with lake surface area, suggesting that atmospheric deposition may be the primary source of cadmium to the lakes. Areal burdens of cadmium varied about 1.5-fold (range: 62 - 92 g $ha^{-1}$) and were strongly correlated with DOC ($r_S = 0.94$), but not with pH, indicating that cadmium transport to the sediments may be related to organic matter.

The effect of whole-lake acidification on the bioaccumulation of cadmium by fish was studied in one of the lakes, Little Rock, which is the site of an experimental pH manipulation project. In September 1984, Little Rock Lake was separated with an impermeable curtain into a reference basin (mean pH 6.1) and a treatment basin that was acidified with sulfuric acid for 2 years to pH 5.6, 2 years to pH 5.2, and 2 years to pH 4.9. Age-1 yellow perch (*Perca flavescens*) were netted annually from each basin in April, after 1 year of residence in the lake, after each year of the pH-5.2 treatment (1988 and 1989) and after each year of the pH-4.9 treatment (1990 and 1991). A random sampling design, stratified by 1-cm total-length groups, was used to sample older yellow perch in April 1989, at the end of the pH-5.2 treatment, and again in April 1991, at the end of the pH-4.9 treatment. Between-basin comparisons of cadmium in whole yellow perch indicated that lake pH significantly influenced cadmium bioaccumulation by fish. After 1 year of residence in the lake, mean whole-body concentrations and burdens of cadmium in age-2 and older fish sampled in 1989 and in 1991 were less in the treatment basin than in the reference basin. The decreased bioaccumulation of cadmium by yellow perch in the acidified treatment basin may reflect increased competition between cadmium and hydrogen ions for binding sites on cell membranes of the gill surface. Estimated cadmium inventories in the yellow perch populations of Little Rock Lake in 1989 were 24 mg in the reference basin and 19 mg in the treatment basin.

# Regional and Seasonal Variability in the Vertical Distribution of Mesozooplankton in the Greenland Sea

**Richter, C. 1994**
**University of Kiel (Germany), 101 pp.**

A large-scale regional and seasonal zooplankton investigation was carried out in the Greenland Sea covering the entire water column down to 3000 m depth. It focussed on the composition and vertical distribution of zooplankton in relation to the hydrographic régime (i) and in course of the year (ii). Sampling was carried out with vertical Multinet hauls (150 µm mesh) in nine depth strata from 3000 m to the surface.

(i) In Atlantic waters, *Calanus finmarchicus* (Calanoida, Copepoda) dominated in abundance (40%) and biomass (55%). In cold Arctic waters of the Greenland Sea Gyre (GSG), *Oithona* (Cyclopoida, Copepoda) was numerically dominant (38%-58%) and *Calanus hyperboreus* in terms of biomass (35%). Highest numbers of individuals were found in the upper 500 m, while a large fraction of the biomass was located below.

(ii) Species composition remained fairly constant throughout the year (48 species) with *Oithona* dominating in abundance (53%) and *C. hyperboreus* in biomass (32%). Integrated abundance varied by a factor of 2.5, with maximum values in June (7.4 $10^5$ $m^{-2}$). Integrated biomass was high (14 g DW $m^{-2}$) and remarkably constant, varying by a factor of 1.5 between the winter minimum and the late summer maximum. Depth was the main factor shaping the community, revealing distinct assemblages of

(1) widely distributed and abundant taxa*(Oithona, Oncaea, Calanus, Pseudocalanus)*

(2) mesopelagic resident taxa of restricted range (Aetideidae, Ostracoda, Chaetognatha)

(3) bathypelagic resident species of restricted range (Cnidaria).

Distribution patterns of (1) and (2) were highlighted and discussed with regard to potential food requirements and storage capacities (body size). Seasonal vertical migrations were marked for herbivorous calanoid copepods. Their extent and timing appeared to be related to body size, both inter- and intraspecifically. *Calanus hyperboreus* carried out extensive vertical migrations exceeding 1500 m, with a brief surface period for the larger stages. The smaller *Pseudocalanus minutus* remained longer at the surface hibernating at intermediate depths. The ubiquitous cyclopoid copepods occurred in high numbers throughout the year, with *Oithona* occupying the epi- and *Oncaea* the meso- and bathypelagial, both reproducing at the surface in early summer.

A rich mesopelagic community of omni- and carnivorous copepods, ostracods and chaetognaths was encountered, showing a seasonally stable vertical partitioning of the water column. It is estimated that a considerable portion of the secondary production goes into the mesopelagic food web, while the bathypelagic zone might serve as a refuge for overwintering herbivore stocks. High overall biomass and low seasonal variability characterize the Greenland Sea Gyre as a remarkably stable system, in spite of marked seasonal variations in food availability.

# Spatial and Temporal Distribution of Mercury and Other Metals in Florida Everglades and Savannas Marsh Flooded Soils

**Rood, B.E. 1993**
**University of Florida, 180 pp.**

Elevated mercury concentrations were identified previously in freshwater fish in the Everglades, Savannas State Reserve, and receiving waters of the Okefenokee Swamp. The goals of this research were to: 1) determine historic baseline concentrations of mercury in wetland soils of the Florida Everglades, Savannas Marsh, and Okefenokee Swamp; 2) determine post-development changes in sedimentary mercury accumulation; and 3) identify the spatial distribution of mercury throughout the Florida Everglades. Sixty sediment cores were retrieved between January 1992 and February 1993, and were analyzed for total mercury, percent solids, and bulk density. Selected cores were analyzed for carbon (total and organic), and additional metals (Cd, Cr, Cu, Fe, Ni, Pb, and Zn), and were chronologically analyzed after radionuclide analysis for $^{210}Pb$ and $^{137}Cs$.

The average mercury concentration in surface sediment (0 - 4 cm) of 121 ng $g^{-1}$ (n=51, 17-411 ng $g^{-1}$) was 2.5 times (0.2-10.6, n=51) higher than corresponding deep sediment (11-17 cm) concentrations. The largest increases were measured in Water Conservation Areas 1 and 2 (WCA1 and WCA2)(3.7 times higher for both) of the Florida Everglades, while Okefenokee Swamp sediment showed the smallest relative increase (1.4). Because concentration data are vulnerable to temporal variations in bulk sediment accumulation rate, the interpretive problem of co-variance was avoided by determining mercury accumulation rates after radionuclide dating. Post-1985 mercury accumulation rates averaged 53 $\mu g\ m^{-2}\ y^{-1}$ (23-141 $\mu g\ m^{-2}\ y^{-1}$) corresponding to a 6.4 (1.6-19.1, n=18) times rate increase since the year 1900. The largest rate increases occurred in WCA1 and WCA2 cores (7.8 and 8.7 times higher, respectively), while the Savannas State Reserve cores showed the smallest rate increase (3.4). Mercury accumulation rates increase starting about 1940, due perhaps to mid-century alteration of the hydrologic structure of the Everglades, and to increased agricultural and urban development to the north and east. There is presently insufficient information regarding regional inputs to quantify any direct causal relationship between mercury accumulation rate increases and regional human activities. However, apparent nonuniform accumulation of mercury in the Everglades hydrologic basins, coupled with increased accumulation rates of other trace metals (Cd, Cr, Cu, Pb, Ni, and Zn), indicate some atmospheric contribution of mercury from regional anthropogenic activities. The findings are similar to trends reported for lakes in Minnesota, Wisconsin, and Sweden. This agreement is significant, perhaps indicating a global process that leads to similar accumulation rates over widely varying geographic regions. This research provides the first data on mercury accumulation in subtropical wetland systems and demonstrates the feasibility of radiochemical dating of wetland cores.

# Metallic Pollution in Estuaries, with Special Reference to the Effects of Tributylin (TBT) and Copper on the Early Life Stages of *Scrobicularia plana* (Mollusca: Bivalvia)

**Ruiz, J.M. 1993**
**University of Plymouth (United Kingdom), 167 pp.**

During the 1980s a decline in populations of the bivalve *Scrobicularia plana* (da Costa) was noted in several U.K. estuaries: tributylin (TBT) was suspected of being the cause although its toxicity to adults could not be demonstrated except at elevated concentrations; disappearance of clam populations has been also observed in other European countries.

Laboratory tests have revealed that:

- D-larvae hatching from embryos after 48 h in TBT concentrations of 188 ng Sn $l^{-1}$ amounted to < 50% of control values, and doses of 364 ng Sn $l^{-1}$ or 20 µg Cu $l^{-1}$ prevented normal development in ≈ 90% of embryos.
- Planktonic veliger larvae exposed for 10 days to nominal TBT doses ≥ 50 ng Sn $l^{-1}$ grew at rates which, at maximum, were one third of that exhibited by controls.
- Settling pediveligers subjected for 30 days to levels of TBT ≥ 70 ng Sn $l^{-1}$ suffered significant mortalities, and postlarvae kept at 23 ng Sn $l^{-1}$ displayed some shell growth which was both substantially reduced and grossly abnormal.
- Exposure for 30 days to ≥ 300 ng Sn $l^{-1}$ or ≥ 20 µg Cu $l^{-1}$ impaired the burying activity in sand of small spat, and juveniles reared in TBT solutions at ≥ 28 ng Sn $l^{-1}$ grew significantly less than those in the control treatment.
- While small spat held in heavy-metal polluted sediment suffered massive mortalities in 12 days, juveniles exposed for 36 days to butylin-contaminated sediment (0.4 µg Sn per gram dry weight) did not display any limited survival, but both their growth and burying activity were significantly reduced relative to those of juveniles kept in control sediments.

It is concluded that in U.K. coastal areas where TBT in water during the summer-autumn months ranged from ≈ 20 ng Sn $l^{-1}$ to ≈ 200 ng Sn $l^{-1}$ (i.e., ≈ 50 - 500 ng TBT $l^{-1}$) and *Scrobicularia plana* populations disappeared or declined markedly, a cause-effect relationship is most likely to exist between the former and the latter through the deleterious effects of the chemical on the early life stages of the clam; in addition, the continued presence of sediment-bound TBT may render mudflats unsuitable for the development of larval and juvenile bivalves.

# Plant-Herbivore Interactions in the Pelagic Zone of Lakes

**Sarnelle, O. 1992**
**University of California at Santa Barbara, 173 pp.**

This dissertation is comprised of three chapters, each dealing with different, but related aspects of the interaction between planktonic herbivores and algae in lakes.

In Chapter 1, I derived predictions about how the magnitude of *Daphnia* effects on total algal biomass should vary across a gradient of enrichment using two, simple predator-prey models. These predictions were then compared with data from a survey of field experiments in temperate lakes. Algal responses to *Daphnia* manipulation were quantified as an Algal Response Factor (ARF), defined as total algal biomass in the low-*Daphnia* treatment divided by total algal biomass in the high-*Daphnia* treatment. Total phosphorus concentration (TP) was used as an index of algal carrying capacity, ranging from 10-460 μg/l over the 22 experiments surveyed. The Algal Response Factor ranged from 1-40 and was a positive, linear function of TP (ARF = -0.14 + 0.08(TP), $r^2 = 0.81$; logARF = -0.81 + 0.83(logTP), $r^2 = 0.75$). Thus, algal carrying capacity, as quantified by TP, explains much of the variation in *Daphnia* effects on total algal biomass across lakes. These results supported the prediction of the simpler model, a two-species, Lotka-Volterra model of pure exploitation. Incorporating the additional complexity of inedible algae into this model did little to improve its predictive power. In addition, a survey of *Daphnia* effects on the proportionate biomass of inedible algae provided no evidence that *Daphnia* grazing typically favors dominance by inedible algae in eutrophic lakes.

In Chapter 2, I examined the effect of *Daphnia* on the distribution and sedimentation of nitrogen and phosphorus in a eutrophic lake. *Daphnia* manipulation in large enclosures, and whole-lake observations before and after a fish kill, showed that intense *Daphnia* grazing produces large elevations in particulate N:P ratios during clear-water periods. The direction of this effect was consistent with expected taxonomic variation among zooplankton in the N:P of excretion, and may help to explain *Daphnia's* suppression of filamentous cyanobacteria (Chapter 3). N and P sedimentation (mg $m^{-2}$ $d^{-1}$) was reduced during *Daphnia*-induced, clear-water periods, despite increases in particle sinking velocities. In addition, there was an unexpected difference between seston N:P and the N:P of settled particles during clear water, which resulted in a *differential* increase in average sinking velocity calculated for PP relative to PN. *Daphnia* effects on N:P later in the season appeared to be opposite to those during clear-water. My data suggest that *Daphnia* grazing can reduce carbonate precipitation (whitings) by controlling algal biomass. Whitings were accompanied by large increases in sedimentary loss rates for TP and elevated TN:TP in the euphotic zone. Thus, *Daphnia* grazing may maintain relatively low TN:TP during the summer in eutrophic, hard-water lakes.

Herbivory can potentially affect the speed and direction of plant succession by favoring the development of a community dominated by grazing-resistant species. In Chapter 3, this idea was tested by examining the effects *Daphnia* on phytoplankton succession. *Daphnia* manipulation in large enclosures, and whole-lake observations before and after a fish kill, showed that intense grazing promoted the transition from edible, spring-bloom species to similarly edible, cryptophyte flagellates. In contrast, *Daphnia* grazing retarded further succession to grazing-resistant, filamentous bluegreens. Thus, the effects of herbivory on algal succession were not predictable from the relative susceptibilities of these algal species to grazing mortality. These results underscore the importance of indirect effects in the herbivore-plant interactions of planktonic communities.

# The Utilization of Radiant Energy by Algae and the Linkages to the Bio-Optical Properties of Marine Phytoplankton

**Schofield, O.M.E. 1993**
**University of California at Santa Barbara, 239 pp.**

Bio-optical models can increase our ability to resolve the temporal/spatial variability in phytoplankton production. The bio-optical models are based on the linkages between watercolumn optical properties, penetration of photosynthetically available radiation, and phytoplankton production. These models require a term for the quantum yield of carbon fixation which is the efficiency with which radiation absorbed by phytoplankton is converted to photosynthate. The quantum yield is difficult to measure and has been assumed to be constant or have a predictable relationship related the *in situ* light field. The quantum yield of carbon fixation has also been assumed to be independent of wavelength. The variability in the magnitude and wavelength-dependency of the quantum yield was assessed. The results are used to comment on the bio-optical productivity models.

The variability in the quantum yield for field populations was measured. The magnitude of the quantum yield was dynamic and empirically unpredictable in the coastal waters of California using traditional oceanographic measurements. Proxy measurements for the quantum yield of carbon fixation will need to be developed to improve the accuracy of the bio-optical models. The quantum yield was wavelength-dependent for field populations and sensitive to community composition of the phytoplankton.

The wavelength-dependency of the quantum yield for carbon fixation was also measured on laboratory cultures of diatoms, prymnesiophytes, and dinoflagellates. In all cases the quantum yield was wavelength-dependent. Both the magnitude and wavelength-dependency of the quantum yield was sensitive to light history of the culture. The wavelength-dependency was determined by presence of photosynthetically incompetent pigments, Emerson enhancement effects, and processes downstream of the photochemical events at the reaction centers. The wavelength-dependency of the bio-optical properties in phytoplankton suggests that the error in photosynthetic rates measured using artificial light sources is large; however the systematic error in using an artificial light source could be assessed if information on the absorption properties of the phytoplankton was available.

# Mechanisms and Rates of Particle Encounter among Suspension Feeders

**Shimeta, J. 1993**
**University of Washington, 210 pp.**

Suspension feeders are common among diverse taxa throughout marine ecosystems. A focus on unifying, physical constraints on particle-capture mechanisms yields insights into functional morphologies as well as predictive understanding of the roles of suspension feeding in trophic and particle dynamics. Common physical constraints of morphology, particle characteristics, and flow environment are found at the level of particle encounter, determining particle availability to suspension feeders. Encounter mechanisms were modeled in terms of rates, contrasting with previous treatments in terms of efficiencies, for cylindrical and spherical morphologies under assumptions of steady, laminar, low appendage Reynolds-number (Re) flow. A minimal clearance rate was predicted for micrometer-sized particles, due to the balance of direct interception and Brownian diffusional encounter. For a variety of protozoans and invertebrates, clearance rates for colloids may greatly exceed those for larger cells in terms of both particle numbers and organic carbon.

Violations of model assumptions were explored empirically. Selective particle encounter was found dependent on Re regime and particle:appendage diameter. Direct-interception rates for an isolated cylinder showed a stronger direct dependence on particle size and a trend of weaker inverse dependence on appendage diameter as Re rose above unity. As particle:appendage diameter rose above 0.1, the dependence of encounter rate on appendage diameter turned from inverse to direct, implying an optimal appendage size for encountering particles of a given size.

Implications of nonuniform flow were studied with planktonic, protozoan suspension feeders in laminar shear fields mimicking turbulence-driven submicroscale shear. While feeding rates of several bacterivorous and herbivorous flagellates and ciliates were unaffected by imposed shear rate, feeding rates of an aloricate choanoflagellate and a heliozoan were directly related to shear rate over an environmentally realistic range. The latter results are likely produced by a direct influence of shear on encounter rates. Spatial and temporal variations in turbulence may affect feeding rates and microbial food-web dynamics in a species-specific manner, with the strongest coupling predicted for slow-swimming and nonmotile protozoans. Despite low body Re, local flow and feeding rates are directly influenced by larger-scale, inertial flow phenomena.

# Bacterial Decomposition of Marine Aggregates and its Biogeochemical Significance

**Smith, D.C. 1994**
**University of California at San Diego, 111 pp.**

Bacteria play an integral role in shaping the ocean's biogeochemistry. It is now generally agreed that bacteria constitute a large, active component of the ocean's biology and that a significant fraction of the organic carbon produced in the ocean is utilized to support their growth. Since bacteria are restricted to the uptake of small molecules, it follows that much of the organic carbon flux is through the dissolved pool. How organic carbon enters this pool is the subject of much of the research presented here. Specifically, the role of bacterial hydrolytic ectoenzymes in mediating the phase transition of organic matter from particulate to dissolved is examined and the consequences are discussed.

Marine snow aggregates were shown to harbor high levels of hydrolytic ectoenzyme activities, up to three orders of magnitude higher than in the bulk sea water. The hydrolysis rates were in excess of the uptake rates of bacteria resulting in most the hydrolysis products entering the dissolved organic carbon pool. Not all enzymes assayed were enriched to the same degree. Protease and phosphatase occurred at much higher levels than a and ß-glucosidases suggesting that nitrogen- and phosphorus-rich compounds are hydrolyzed faster than carbon-rich compounds. This 'enzymatic fractionation' may explain the observed increases in C/N and C/P ratios of particulate organic matter with depth.

The role of bacterial hydrolytic ectoenzymes in carbon fluxes during a phytoplankton bloom was examined in a mesocosm. Despite the absence of metazoan grazers (which are thought to be critical in making organic matter available to bacteria through their feeding activities), 40 - 65% of the organic carbon produced during the bloom was utilized by the bacteria. This was apparently due to the high levels of hydrolytic ectoenzymes expressed by the bacteria. It is also suggested that the hydrolytic ectoenzyme activities of bacteria attached to diatoms reduced diatom aggregation thereby prolonging the bloom.

It is concluded that much the shaping of the ocean's biogeochemistry by bacteria is through the expression of hydrolytic ectoenzymes and their role in changing the chemical composition and size spectrum of organic matter in the ocean.

# The Importance of Fine-Scale Flow Processes and Food Availability in the Maintenance of Soft-Sediment Communities

**Snelgrove, P.V.R. 1993**
**Massachusetts Institute of Technology, 438 pp.**

To test whether near-bed hydrodynamics modify larval settlement, field and flume experiments were conducted where larval settlement was compared between microdepositional environments (small depressions) and non-trapping environments (flush treatments). Flume flow simulations with the polychaete *Capitella* sp. I and the bivalve *Mulinia lateralis* demonstrated that although larvae of both species were generally able to actively select a high-organic sediment typical of adult habitats over a low-organic alternative with a comparable grain size, elevated densities of both species were observed in depressions for a given sediment treatment. In field experiments carried out in Buzzards Bay, Massachusetts, significantly higher densities of *Mediomastus ambiseta* juveniles, spionid polychaete juveniles, bivalves, gastropod larvae, and nemerteans were observed in depressions compared with flush treatments over 5 experimental periods (3-4 days each) during the summer of 1990, suggesting that larvae were passively entrained in depressions. These experiments suggest that near-bed hydrodynamics may modify settlement at some scales, and that both active and passive processes may determine larval distributions in shallow-water, muddy habitats. In a deep-sea habitat near St. Croix at 900 m depth, the Johnson-SeaLink submersible was used to deploy experiments designed to test the role of larval habitat selection for different patch types versus near-bed flow effects. Densities of colonizers in flush sediment-tray treatments were higher than in depression treatments for total individuals and dominant colonizers, suggesting that passive entrainment did not occur and habitat selection was highly active. Experiments comparing larval response to different types of enrichments (no enrichment, enrichment with *Thalassiosira* sp. or *Sargassum* sp.) over different periods of time (23 days or 29 months) indicated that different species respond depending on type of organic matter and duration of deployment. These findings support the hypothesis that small-scale patches create microhabitats for colonizing species, thus reducing competitive interactions and enhancing species richness. Small-scale patches of different organic composition and age may therefore be an important and variable resource contributing to the immense species diversity that has recently been reported for deep-sea habitats.

# Harvesting and Utilization of Light by Hermatypic Corals

**Stambler, N. 1992**
**Bar-Ilan University (Israel), 221 pp.**

Hermatypic, zooxanthellate corals are limited to the euphotic zone in tropical seas. Corals, like any other object, will absorb a variable fraction of the total radiant flux incident upon them, depending on their shape, orientation, and absorbency. The remaining light will be scattered or reflected. An integrating (Ulbricht) sphere was used to measure the fraction of the incident quantum flux that is absorbed by a coral colony introduced into the integrating sphere.

In branched colonies shading among branches reduces the absorbed light per unit area and/or per zooxanthella. Therefore, under low irradiance, it is advantageous for colonies of branched species to flatten out and reduce branching to one plane, perpendicular to the light. Increasing in algal density, will increase the light absorbed by the corals until that density will cause an intercellular "packaging effect" among the zooxanthellae. The *in vivo* spectral average-chlorophyll *a* absorption cross section, *a, as found in the coral, decrease with increasing chlorophyll density.

The coral responds to both low light intensity and to nutrient enrichment by increasing the amount of chlorophyll $cm^{-2}$. The increase of chlorophyll under light resulted from increasing chlorophyll per algal cell. The response of the coral to nutrient enrichment is mostly due to the increase in the number of algae $cm^{-2}$. This increase in algae $cm^{-2}$ also caused an increase in chlorophyll $cell^{-1}$ due to increase shading. In total darkness there is a loss of chlorophyll and of zooxanthellae.

The corals that have high concentrations of chlorophyll in both nutrient-enriched and shade-adapted colonies absorbed more light compared to colonies with low pigmentation. In the case of low light there is an adaptation of the photosynthetic apparatus of the algae and the quantum yield is high. In contrast, nutrient-enriched colonies have low light-utilization efficiency because of a low rate of photosynthesis. Photosynthetic rates, on a per-cell basis, were inversely correlated with algal densities, indicating possible competition among the algae for $CO_2$.

Eutrophication reduced the contribution of the zooxanthellae to the host. The algae overgrow their host and the skeletal growth rate of the colonies is slowed down. Corals dominate shallow coastal regions in tropical oceans. In these oligotrophic waters they success under a wide range of irradiance levels.

# The Use of Mesopelagic Detritus by Zooplankton in Monterey Bay, California

**Steinberg, D.K. 1993**
**University of California at Santa Cruz, 163 pp.**

The mucus feeding structures or "houses" of the giant larvacean *Bathochordaeus* provide model systems for the study of deep-sea detrital communities, particularly the poorly known zooplankton associates of detritus. This dissertation examines the role of detritus or "marine snow" as a habitat and food source for mid-water zooplankton communities, as well as the importance of particle-associated zooplankton in remineralization of particulate organic carbon in the mesopelagic zone. Zooplankton communities on detritus have been largely undetected to date, mostly due to sampling difficulties. For this dissertation, houses were sampled between 100 and 500m in Monterey Bay, CA, using a submersible ROV (remotely operated vehicle).

A unique zooplankton community occurs on giant larvacean houses, and houses are enriched in zooplankton compared to surrounding waters. Copepods are the dominant associates (e.g. *Oncaea*, *Scopalatum*, and *Microsetella*) and many of the species possess benthic-like morphology and feeding adaptations. Investigation of the feeding habits of one of the house-associated copepods, *Scopalatum vorax*, shows that it feeds on both microbial and metazoan associates of larvacean houses, and possibly the house-mucus matrix itself. This consumption of detritus at depth indicates that metazoans contribute to remineralization of particulate organic carbon in the mesopelagic zone.

The biological processes that mediate remineralization of particulate organic carbon in the mesopelagic zone, decomposition by bacteria and grazing by metazoans, were also studied using larvacean houses. Houses are sites of elevated metabolic activity compared to surrounding waters, with rates of remineralization similar to loss rates reported in previous investigations of material decay in sediment traps. In addition, zooplankton are estimated to contribute proportionately more to house remineralization than bacteria, and zooplankton consume and alter a substantial part of the house before it sinks out of the mesopelagic zone.

This dissertation reveals that mesopelagic detritus provides a benthic-like habitat and serves as a feeding center for mid-water zooplankton. Some of these zooplankton may be "swimmers" previously excluded from sediment trap analyses. Most importantly, particle-associated zooplankton can be important in remineralization and transformation of particulate organic carbon in the mesopelagic zone.

# Sulfide-Dependent Oxidative Stress in Marine Invertebrates, Especially Thiotrophic Symbioses

**Tapley, D.W. 1993**
**University of Maine, 160 pp.**

Animals that harbor symbiotic sulfide-oxidizing chemoautotrophic bacteria (thiotrophic symbioses) must expose themselves to both oxygen and sulfide to provide these substrates to their symbionts. The production of free radicals during sulfide oxidation has previously been proposed, but not proven, and if true, this could impose an oxidative stress on these symbioses. Here, I show that that both oxygen- and sulfur-centered free radicals are produced during sulfide autoxidation, and that this does impose an oxidative stress on organisms. Activities of antioxidant enzymes in animal tissues of the symbiotic bivalve *Solemya velum* and the related but non-symbiotic protobranch *Yoldia limatula* increase following simultaneous exposure to oxygen and sulfide. Furthermore, I present evidence that low-molecular-weight compounds, particularly glutathione, are important antioxidants in these animals.

In addition to these radicals, sulfide autoxidation produces substantial chemiluminescence. This sulfide-dependent chemiluminescence may explain light emission by the deep-sea hydrothermal vents.

Most superoxide dismutase activity in *S. velum* derives from the mangano- form of the enzyme, which in eukaryotes is usually restricted to the mitochondria. The unusual proportion of Mn-SOD in this clam may be owing to the need to maintain activity in the face of chronic sulfide exposure, since the usual cytosolic cupro-zinc SOD is inhibited by sulfide, whereas Mn-SOD is probably not.

Tissue homogenates from these clams and from three phylogenetically diverse species of hydrothermal vent invertebrates are able to suppress the formation of free radicals during sulfide autoxidation to differing degrees. In general, tissues from species which are from the highest sulfide environments (*S. velum, Riftia pachyptila*, and *Bythograea thermydron*) suppress radical formation in the presence of 1 mM sulfide, whereas those from species (*Y. limatula* and *Bathymodiolus thermophilus*) which inhabit environments having lower levels of sulfide cannot. This does not mean that defenses of the latter species are insufficient to protect against sulfide-dependent oxidative stress, because these species probably never experience sulfide concentrations as high as 1 mM. Rather, the interspecific difference indicates that these defenses are particularly robust in those species which obligately experience high sulfide concentrations.

# The Ecological Effects of Experimental Acidification upon Littoral Algal Associations of Lakes in the Boreal Forest

**Turner, M.A. 1993**
**University of Manitoba (Canada), 194 pp.**

This research evaluated the effects of acidification upon littoral algal associations in studies conducted at the Experimental Lakes Area in northwestern Ontario, Canada. The investigations included: experimental whole-lake sulfuric and nitric acidification, experimental whole-lake nutrient additions, and surveys of lakes varying in nutrient concentrations. Two principal littoral algal associations were studied: epilithon (association on rock surfaces), and metaphyton (algal community associated with, but unconstrained by, a surface).

Nutrient controls of littoral and planktonic algal photosynthesis differed greatly due largely to the diffusive resistance to benthic uptake of dissolved inorganic carbon (DIC). Epilithic net photosynthesis declined as a result of acidification altering the carbon cycle. With a parallel increase in epilithic respiration, the energy balance within epilithon became unfavourable (i.e. respiration as a fraction of 'gross' photosynthesis increased) causing decline of this association. This dysfunction serves as an early warning of metabolic imbalance in lakes, which are more sensitive to acidification than previously thought.

Filamentous green algae (FGA) of the Zygnematales proliferated in the littoral zone initially as periphyton, and later as metaphyton, as acidification progressed. FGA had high photosynthetic capacity, displaying an energy balance similar to unacidified epilithon. Their growth was controlled negatively by density-dependent feedback, and positively by light intensity, DIC, water movement, and temperature. FGA biomass varied seasonally, being at a minimum in spring, and reaching an annual maximum in early fall.

FGA blooms, sometimes reaching 30 cm in thickness, affected several aspects of the littoral zone both positively and negatively. Large intra- and interannual variability diminished their ability to compensate for acidification-induced oligotrophication otherwise seen in the littoral zone. The FGA were sometimes the largest epilimnetic phosphorus-containing compartment. Their nitrogen dynamics caused both lake-wide acidification (spring and summer) and alkalinization (fall). Blooms attenuated light available to other phytobenthos by as much as 90%. The FGA provided seasonal habitat for animals, but respiration- and decomposition-related oxygen depletion posed potential risks for inhabitants. FGA in acid lakes will likely proliferate further as human activities release the algae from several growth limitations by increasing nutrient availability (e.g. $CO_2$), by increasing water temperatures, and by extending their growing season.

# A Preliminary Study on Some Plankters along the Turkish Black Sea Coast: Species Composition and Spatial Distribution

**Uysal, Z. 1993**
**Middle East Technical University (Turkey), 138 pp.**

In order to acquire information on the pelagic microscopic community composed primarily of Diatomae, Dinoflagellata and some species of Chlorophyta, a baseline study is carried out along the Turkish coastal waters of the Black Sea. Scarcely found species of Cyanophyta, Chrysophyta and of classis Ciliata (tintinnids) of zooplankton had minor importance. Among all these groups diatoms dominated both qualitative and quantitatively and followed by dinoflagellates.

Analysis of multispecies plankton data via multi-dimensional scaling (MDS) technique and the associated physico-chemical variables for each sampling period have shown formation of different plankton patches along the coast. Such patterns are reported for the first time to planktonic communities in the southern Black Sea in addition to species composition and their quantitative dynamics. Surface spatial distribution of plankters were affected much from both prevailing surface currents and mesoscale eddies attached to the shelf and are in relation with biochemical parameters such as, ortho-phosphate, silicate, dissolved oxygen, total organic carbon and chlorophyll-*a*. The blooming of plankters in the region between Bosphorus junction of the Black Sea and Sakarya River front was found to be peculiar to this region having less contribution from the Romanian and Bulgarian coasts. In the whole, western part of the Turkish coast is richer both qualitative and quantitatively than eastern sector. Characteristic features of the blooming sites were lower proportional representation (J') among the species and diversity (H') due to intense flowering of dominant species. Higher figures in terms of cell density and number of species at surface are apparent features of the west coast when compared to the eastern part, however, there is much homogeneity (equitability) within species encountered in the eastern part.

Depthwise species assamblages have shown that, variation in species diversity with depth to a certain degree (down to 40-50 meters) is negligible. From the distribution of discriminating species, it could be concluded also that the western community differs greatly from the eastern community.

# Food Web Relations of Littoral Macro- and Meiobenthos

**van de Bund, W.J. 1994**
**University of Amsterdam (Netherlands), 107 pp.**

The thesis addresses factors regulating populations of chironomid larvae and chydorid cladocerans, focusing on factors associated with food availability. A comparative field study identified these organisms as the principle representants of the macro- and meiofauna inhabiting the sandy littoral zone of lakes.

Field work concentrated on characterization of spatial heterogeneity and seasonal variation. Chironomid and chydorid distributions were highly patchy; wind-induced disturbance had strong and species-specific effects on patchiness. Generally, seasonal and spatial correlations were higher among chironomids or chydorids than between members of these groups. Competition among early larval stages was found very important for chironomid population regulation, causing a difference in the timing of their development between two sampling sites where settling densities differed. This persisted throughout the season, having important consequences for the impact of fish predation later in the season. At one site, larvae were already in the fourth instar at the onset of predation; these larvae burrow so deep that they are out of reach of the fish. At another site they were still in surface sediment layer, resulting in higher predation losses.

Laboratory experiments clarified the potential importance of interactions between chironomids and chydorids. Chydorids negatively affected the growth rate of second-instar chironomids. Chironomid larvae stimulated the parthenogenetic reproduction of chydorids; feeding experiments showed that this is likely to be caused by the chydorids feeding on chironomid faecal material. Microcosm experiments were performed studying the impact of three profundal deposit-feeders with different feeding modes on the abundance and production of sediment bacteria. Bacterial production in surficial sediment increased significantly. Since mechanical stirring the sediment had a similar effect, it was concluded that this was caused by physical disturbance of the sediment, and not direct grazing. Changes in bacterial abundance appeared to be species-specific, reflecting differences in feeding and/or foraging behaviour.

The results emphasize the key role of detrivorous macro- and meiobenthos in the benthic food web of lakes. The fate of bottom detritus is strongly affected by bioturbation and partial digestion by detrivores. Competition for a limited supply of detritus is a crucial factor in the seasonal development of chironomids, especially during early phases of their life-cycle. The close connection of detrivory, mineralization and predation lake sediments was demonstrated.

# The Effects of Temperature, Light, Season, and Body Size on the Photosynthesis and Respiration of Zooxanthellae and Zoochlorellae Symbiotic within *Anthopleura Elegantissima* (Brandt)

**Verde, E.A. 1993**
**Florida Institute of Technology, 86 pp.**

The clonal anemone, *Anthopleura elegantissima*, is the dominant cnidarian in the intertidal zone of the Pacific Northwest. This anemone is unique because it is one of two temperate cnidarian species that harbors, intracellularly, two distinctly different algal photosymbionts: zooxanthellae (ZX) and zoochlorellae (ZC). The purpose of this investigation was to compare any differences in physiological patterns of ZX and ZC in *A. elegantissima* to determine the reason(s) for the maintenance of two such symbionts.

The effects of temperature, light intensity, season, and anemone size on algal production and respiration within anemones were investigated. Both photosynthesis and respiration were measured by a computer-controlled underwater respirometer equipped with a light sensor and oxygen electrodes to measure daily oxygen flux of the intact association.

The results of this study suggest that ZX are the "superior" symbionts since they display greater photosynthetic rates and presumably higher translocation rates. As temperature and light intensity increase, the productivity of ZX-bearing anemones increases faster than that of ZC-bearing anemones. The photosynthetic rates of ZX-bearing anemones were also higher than that of ZC-bearing anemones during much of the year. Regardless of algal species, summer productivity rates were higher than winter productivity rates due to a combination of higher light intensities and temperatures. Regardless of season, photosynthetic rates of algae in small anemones were higher than that of algae in large anemones.

Both environmental and biological parameters may contribute to and modulate the distribution of ZX- and ZC-bearing anemones within the intertidal zone. High light intensities, coupled with elevated temperatures, promotes ZX-anemone associations. In contrast, low light and temperature regimes provide ZC with a potentially higher competitive advantage due to their high intrinsic growth rate.

# Ecological Aspects of Iron Acquisition in *Synechococcus* Spp. (Cyanophyceae)

**Wilhelm, S.W. 1994**
**University of Western Ontario (Canada), 196 pp.**

As primary producers, marine cyanobacteria regulate the biological and biogeochemical cycles of aquatic ecosystems and influence ocean-atmosphere gas exchange. The purposes of this project were to determine if a *Synechococcus* sp. was capable of utilizing a high-affinity iron transport system during periods of iron-limited growth and if physiological changes due to iron limitation could be identified. Resolution of these factors was achieved by maintaining the cyanobacterium *Synechococcus* sp. PCC 7002 in continuous culture over a range of iron availabilities.

Changes in physiology were detected over a range of iron concentrations. Reductions in cellular pigments were accompanied by a deterioration of thylakoid integrity and changes in cellular carboxysome and polyphosphate bodies. Polypeptide profiles of thylakoid, cytoplasmic, and outer membrane fractions demonstrated an enhanced production of specific proteins during iron-limited growth. Photosynthetic efficacies (measured as oxygen evolution and carbon fixation) are significantly reduced during iron-limitation, with carbon incorporation being reduced from luxury levels to the minimum requirements for cellular carbon turnover.

Steady state cell densities within chemostats, combined with growth data obtained from batch cultures, demonstrate a non-linear response between iron concentration and cyanobacterial proliferation. Results suggest that this is brought about by changes in the cellular iron quotient, coupled with the activation of an energy dependant high-affinity iron transport system. The activation of this system involves the release of four novel iron-regulated, iron-binding cell products (siderophores) by *Synechococcus* sp. PCC 7002.

To determine the prevalence of siderophore production, ten species of cyanobacteria were examined for the ability to produce siderophores under iron-limiting conditions. In all cases these cyanobacteria were found to produce siderophores, and, in many species, the production of multiple siderophores was detected. Analysis of the chemical moieties associated with these compounds demonstrated that hydroxamate-type, catechol-type, and atypical-type iron chelators are produced by these cyanobacteria. The presence of siderophores enhances the ability of cyanobacteria, grown under iron-limiting conditions, to assimilate iron via membrane-associated receptor proteins. Ferrisiderophore receptors are not expressed by cyanobacteria grown under iron-replete conditions.

An amalgamation of these results infers that some cyanobacteria utilize high-affinity iron transport systems, involving the serial transport of iron via soluble and membrane-associated ferrisiderophore complexes, in a process which requires the presence of membrane-specific receptors and ATP. This work demonstrates that the definition of affinity in iron transport must consider the biologically available and unavailable pools of iron in the environment. This work suggests that high-affinity iron transport in cyanobacteria involves the conversion of biologically unavailable iron to an available form.

# Investigations into the Influence of Microphytobenthos on Nutrient Fluxes at the Sediment-Water Interface in the Tidal River Elbe

**Wiltshire, K.H. 1992**
**University of Hamburg (Germany), 186 pp.**

The influence of microphytobenthos on nutrient and oxygen fluxes in porewaters and shallow overlying waters, respectively, were examined for sediment-water systems of the Elbe Estuary, Northern Germany. The methods implemented were incubation methods with dark/light phases, in combination with microelectrode measurements. A mathematical model was developed for the detailed description of oxygen/nitrate profiles during periods when photosynthesis occured in the upper sediment layer and during dark periods. Sediment sectioning techniques were developed for the fine definition of porewater profiles. A High Pressure Liquid Chromatography method was adapted for pigment analysis in sediments.

Gross fluxes of oxygen of -30 to 170 $mmol \cdot m^{-2} \cdot d^{-1}$ were measured during algal production phases (net fluxes into the water: -9 to -160 $mmol \cdot m^{-2} \cdot d^{-1}$). The gross production and the net production rates within the sediment were $7 \cdot 10^{-6}$ $mmol \cdot cm^{-3} \cdot s^{-1}$ and $4 \cdot 10^{-7}$ $mmol \cdot cm^{-3} \cdot s^{-1}$ respectively. During the dark phases of the incubations fluxes into the sediment of 20 to 90 $mmol \cdot m^{-2} \cdot d^{-1}$ were measured. The corresponding oxygen consumption rates were about $4 \cdot 10^{-7}$ $mmol.cm^{-3} \cdot s^{-1}$. The oxygen pentration depth was between 0.16 and 0.4 cm during periods of photosynthesis.

A two-layer mathematical model was used in all the experiments for the simulation of oxygen profiles in the sediments using the experimental results obtained as a basis. The data and profiles obtained using the model are in good agreement with the measured data when diffusion coefficients of 2 to $4 \cdot 10^{-5} \cdot cm^2 \cdot s^{-1}$ are used and the photic layer is designated a thickness of 0.08 - 0.09 cm.

Concentration measurements for nitrate-N in the water above the incubated sediments showed net fluxes of 0 to -105 $mmol \cdot m^{-2} \cdot d^{-1}$ out of the sediments during the illuminated incubation phases. During the dark phases net fluxes were directed from the water to the sediment. Porewater analyses clearly showed that the nitrate penetration depth was significantly deeper in those cores incubated with light than those incubated without. This effect is due to the inhibition of denitrification and/or the stimulation of nitrification. This is a direct result of greater oxygen sediment penetration as a result of benthic photosynthesis.

Effects resulting from algal nutrient uptake were too small with respect to mineralisation processes in the sediment to be observed.

The results from this work clearly show that all future considerations on the oxygen and nitrogen budgets of the tidal Elbe Estuary must include the effects which microphytobenthos can have on the transformation processes of these elements.

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